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ON THE ANATOMY AND PHYSIOLOGY OF PROTOPTERUS ANNECTENS.

BY W. N. PARKER, PH.D., Professor of Biology in the University College of South Wales and Monmouthshire, Cardiff.

PLATES VII. TO XVII.

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III.

ON THE ANATOMY AND PHYSIOLOGY OF PROTOPTERUS ANNECTENS.

By W. N. PARKER, Ph.D., F.Z.S., Professor of Biology in the University College of South Wales and Monmouthshire, Cardiff. (Plates VII. to XVII.)

(COMMUNICATED BY PROFESSOR A. C. HADDON, M.A.)

[Read April 11, 1892.]

INTRODUCTION.

The work which has resulted in the present Paper* was begun in Freiburg im Breisgau in the summer of 1888, when I was fortunate enough to obtain a number of fresh specimens of Protopterus. As so many new and interesting points then presented themselves, I ventured to publish a short preliminary account of my observations (21) in the following autumn, without, however, giving any figures.

Although many previous observers have described the structure of Protopterus, they had in most cases the disadvantage of working upon badly preserved material, and I have therefore thought it advisable to illustrate the anatomy of this important type somewhat fully, except in the case of those organs which had already been worked out more completely. Thus, with the exception of a few brief references to certain details the present Paper does not touch upon the general

* There has, unfortunately, been a considerable delay in the publication of this Paper, which was finished in the spring of 1891; it has, therefore, only been possible to insert references in notes in the proof to one or two of the more important papers which have appeared since then. An abstract has already appeared in the "Proceedings of the Royal Society," vol. xlix., p. 549. 1891.

structure of the skeleton and the muscular and nervous systems.* Moreover, as I found that, on account of the many interruptions which have occurred during the progress of the work, and the limited time at my disposal, a detailed study of the histology of this animal was likely to postpone indefinitely the publication of my Paper, and to make it of an inordinate length, I have thought it better to leave several interesting points aside for the present. It should be mentioned that Protopterus is well adapted for minute histological investigation, chiefly on account of the large size of the elements, and the extreme vitality of the tissues.

Besides numerous dissections and sections of the various parts and organs, I made a complete series of about 2250 transverse sections, from the snout to the root of the tail, of a young female specimen, 8 cm. in length, and about 1 cm. in dorso-ventral diameter. These were extremely valuable in checking the work throughout.

This specimen was preserved in chromic acid, to which a few drops of

* For papers referring to these parts compare the bibliography given by Baur (2). Amongst the more important may be mentioned 9, 14, 16, 18, 20, 24, 29; and, treating specially of the brain and cranial nerves :—

H. BEAUREGARD, . . "Encephale et nerfs crâniens du *Ceratodus fosteri*."—Jour. de l'Anat. at de la Physiol. 1881.

G. FULLIQUET, . . "Recherches sur le cerveau du *Protopterus annectens*."—Dissertation presenté a la faculté des Sciences pour obtenir la grade de Docteur. Genève, 1886.

SERRES, . . . "Recherche sur quelques points de l'organisation du *Lepidosiren annectens*; description du cerveau."—Comptes rendus de l'Acad. des Sciences de Paris, tome LVII., No. 12 et 13. 1863.

SANDERS, . . . "Dipnoan brain."—Proc. Roy. Soc., vol. 43.

J. W. VAN WIGHE, . "Ueb. d. Visceralskelet u. die Nerven des Kopfes der Ganoiden u. von Ceratodus."—Niederl. Arch. f. Zool., v., Bd. 3.

It appears that the brain of the Dipnoi, though showing considerable similarity in certain points to that of the Amphibia, possesses many special characters.

I should add that in Protopterus I have not succeeded in finding a sympathetic—not even such rudimentary traces as have been described in Petromyzon by Dohrn ("Stud. z. Urgesch. d. Wirbelthierkörpers," XIII.—Mittheil. a. d. zool. Stat. zu Neapel., Bd. VIII., 1888). A sympathetic is not known to exist in the other genera of Dipnoi.

nitric acid had been added, as the former alone is not sufficient to decalcify the hard bone. It was then cut into several pieces, each of which was stained entire with borax carmine, and cut into sections in a Jung's microtome. Various methods of preparation were used for the individual parts (see the explanation of Plates). Of these, I found that on the whole the most satisfactory was preservation in corrosive sublimate, and staining first with picric acid, and then with alum carmine. But unfortunately I did not try this method until my material was nearly exhausted.

It should be noted that my researches were made on specimens either directly after their removal from the "cocoon," or after they had been active at most for two or three weeks.

I beg to offer my sincere thanks to the Council of the Royal Society for the grant out of which various expenses connected with the investigation were defrayed, as well as for a second donation to aid in its publication. To Professor Wiedersheim I am indebted, not only for his generosity in supplying me with abundant material, but also for his constant and never-failing help and advice during the progress of the work. I must also thank my friend Prof. Howes for many valuable suggestions.

All my material, with the exception of two specimens, purchased last autumn, were placed at my disposal by Professor Wiedersheim. These were received alive direct from the neighbourhood of the Gambia, and to Dr. J. Beard is due the credit of having arranged for their transport. While in the torpid condition about one hundred specimens had been dug out, each surrounded by a clod of earth, and the clods were then packed together in open crates. In this manner they travelled without harm, nearly all of them being alive and in a healthy condition on their arrival in Freiburg. On being removed from the clods, they were, by the kind permission of Professor Hildebrandt, placed in a large wire cage, sunk beneath the water in a basin used for the culture of water plants in one of the hot-houses of the Botanical Gardens, in which a constant temperature of 22·5° C. was maintained.* That they can exist for a long time

* Since my preliminary Paper (21) was published, an interesting account of the habits of Protopterus in its natural state has been given by Stuhlmann (25), who mentions that during his his stay in Quelimane, the water in which the animals were found had a temperature of 29–37° C.

within the clods if the latter are not allowed to get too dry was shown by Hawkins in 1856 (*Illustrated News*, Suppl., Sept. 20th, 1856, quoted by Gray, 6), who states that his specimens had passed eight months in this condition.

The largest of the specimens I had the opportunity of observing for a few seconds only, as it escaped into the tank; it must have been, roughly, about 80 cm. in length, while the smallest ones were not more than 8 cm. The measurements given by other observers are within these limits. Stuhlmann (25) states that the greater number of his specimens were between 20 and 40 cm., the largest being only 68 cm. It is interesting to note that comparatively small specimens are sexually mature. I found ripe spermatozoa and fully-formed ova in some which were certainly under a foot long. From these facts it seems probable that Protopterus lives to a great age; and this supposition is supported by the somewhat incredible statement of the natives mentioned by Stuhlmann that some specimens reach a length of six feet.* From the observations of Hyrtl (12) and Bischoff (4) it appears that Lepidosiren also attains a large size, reaching, at any rate, three feet in length.

Our specimens were fed at first with Entomostraca, water-snails, and earthworms, but as they soon began to bite one another viciously, this diet seemed to be insufficient for them, and they were supplied with small white fish (Leuciscus); but they still continued to bite and kill one another. These observations, as well as those of Bartlett (see Gray 6), M'Donnell (18), and Stuhlmann (25), show that Protopterus is mainly a flesh-eater, although apparently not exclusively so; there is no need, therefore, to suppose, as Ayers (1) has done, that a change of habit has taken place in this respect. In spite of their great voracity, they seem to be able to fast for considerable periods without harm (Stuhlmann). From Bartlett's observations they appear to grow rapidly: he states that a specimen which, when taken out of its cocoon, measured nine inches in length, grew in three months to a length of eighteen inches.

It is extremely difficult to keep these animals alive for observation in captivity for any length of time, owing to their habit of killing and eating

* Günther ("Study of Fishes") also states that Protopterus attains a length of six feet.

one another, even when they are supplied with an abundance of food. The bite from their scissor-like teeth causes terrible wounds. Some of our specimens were nearly bitten in two, the bites being mostly through the muscles of the back. But even when badly wounded the injured individuals often lived for some days, until they finally succumbed from loss of blood. Their vitality is extraordinary; even after having been chloroformed and injected, and the brain and spinal cord separated, they may again begin to move energetically. The head of one such apparently dead specimen when separated from the trunk, and after the removal of half the lower jaw, held the scissors firmly in its mouth by the other half when I attempted to cut away the latter. These observations are fully supported by Stuhlmann, and it is interesting to compare them with the experiments made by Steiner on Elasmobranchs (Scyllium and Mustelus).*

Although I had not the opportunity of observing the mode of feeding of Protopterus, it seems that the prey is first bitten through and then eaten bit by bit. From the structure of the alimentary apparatus it is improbable that very large mouthfuls can be swallowed. Krauss (16) has observed the manner in which the food (Hydrophilus) was chewed before being swallowed.

Protopterus appears to be most active at night, and to prefer shallow water (Stuhlmann). When moving about slowly on the bottom, the two fins of each side are usually used alternately, those of one side pointing forwards while those of the other extend backwards, though there appears to be no strict regularity in their movements. The filamentous extremities, which can be of little use in swimming, certainly seem important in creeping along the bottom, and it is interesting to notice that the movements more nearly resemble walking with alternate steps than swimming with simultaneous strokes of the fins of both sides. Gray (6) has compared these movements with those of a Triton, and several other observers have noticed them. The powerful tail forms a most efficient organ for swimming rapidly through the water.

* "Ueb. das Centralnervensystem d. grünen Eidesche, nebst weiteren Untersuch. üb. das des Haifisches."—Sitz. Ber. d. K. Preuss. Acad. d. Wissenschaften zu Berlin, Bd. XXXII. 1886.

It is well known that Protopterus comes to the surface to breathe at short intervals, and thus it is evident that the lungs perform an important, if not the chief part in respiration during the active life of the animal. The air passes out again through the opercular aperture, and the movements of the operculum itself indicate the fact that branchial as well as pulmonary respiration takes place.

I have been unable to notice any external characters which distinguish the sexes from one another, and it is therefore not easy to give any reliable data as to the proportion between the sexes. In immature individuals it is even difficult to distinguish the ovary from the testis without microscopical examination. And as the generative organs of the male were described for the first time in my preliminary paper (21), the previous statements with regard to the relative proportionate numbers of male and female individuals are valueless. My own observations indicated that females, and those of Stuhlmann that males, are the more abundant.

Had our specimens not been required for breeding purposes they would naturally not have been left together after their cannibal instincts had asserted themselves. But, as it was, very few were living eight weeks after their arrival, and even these few died soon afterwards.

It is obvious from Stuhlmann's observations that the breeding time of Protopterus in Quelimane must be between January and July, during which time the animal lives a free existence.*

* Ayers (1) gives the following note in his Paper, without, however, stating his authority: "Die Thiere paaren sich im August, und laichen 6 bis 10 Fuss tief im Wasser, in flachen Gruben, die zur Aufnahme der Eier in schlammingen Ufern ausgehölt sind. Man hat die jungen künstlich ausgebrütet und gefunden, dass sie den Kaulquappen von *Rana* in ihrem äusseren Character gleichen. Männchen und Weibchen sind während der Laichzeit stets bei einander."

Fins.

Paired Fins.

The filamentous paired fins of Protopterus are evidently greatly degenerated structures. The pectoral are longer than the pelvic members, but more or less of the free ends of both pairs are often lost, and are probably bitten off by other individuals. It is highly probable that the lost parts can be regenerated.* As already stated, they are used more like limbs for walking than fins for swimming, but this physiological resemblance to the limbs of the higher animals is not borne out by a morphological one; the fin is an ichthyopterygium, and shows no tendency towards modification in the direction of a cheiropterygium. A finfold supported by jointed cartilages and horny rays is present on both fins except in their proximal and distal parts.

Scales are absent on the fins, the epidermis of which is similar to that covering the body, except that goblet-cells are less numerous, and multicellular glands and sensory organs are absent (see pp. 120, 121). The supposition, therefore, that the limbs of Protopterus serve as "feelers" † is not borne out by a study of their structure. The nerve supply seems out of all proportion to the rudimentary muscles, and this fact renders the absence of sensory organs all the more surprising.

Wiedersheim has described and figured the brachial plexus, and states (29) that it is formed by the vagus, the double hypoglossal (which has dorsal and ventral roots) ‡ and the first spinal nerve; and that the

* Since writing the above, Professor Howes has informed me that Mr. Boulanger has recently obtained proof of the regeneration of the fins. His Paper was read before the Zoological Society in February, 1891 (Proc. Zool. Soc., 1891, p. 147; *cf.* also, Catherine Hopley, Amer. Nat., xxv., 1891). The bifid fin described by Albrecht (Sitzungsberichte d. Berlin Akad., 1886, p. 545) was probably a regenerated one (8).

† See Owen (20), and W. Bateson, "The Sense-Organs and Perception of Fishes."—Journ. Marine Biol. Assoc., New Series, vol. i., p. 225. 1890.

‡ Iversen, "Bemerk. üb. die dorsalen Wurzeln des Nervus hypoglossus."—Berichte d. naturforsch. Gesellsch. zu Freiburg i. Br., Bd. II., p. 33. 1887.

latter passes internally, and the hypoglossal externally to the cranial rib, on the anterior side of which, about half-way between its proximal and distal ends, the two unite with the vagus to form the brachial nerve. My examination of these parts has had reference chiefly to certain branches of the vagus; but from my preparations it appears that all the nerves that go to form the brachial plexus lie internally to the cranial rib, though as they originate rather externally to its articulation with the skull, they curve round and partially encircle it (see Pl. XVII., fig. 71). The hypoglossals unite with one another, and the nerve thus formed gives off a branch to the muscles of the cranial rib, and then joins the first three spinal nerves (Iversen), the compound nerve thus formed immediately uniting with the brachial branch of the vagus * to form the single brachial nerve.

The nerve supply of the pelvic fin has been figured, though not described, by Humphry (9), who shows several nerves converging on the dorsal aspect of the fin to form a single trunk, which passes into the extremity. Dissections show that each pelvic fin is supplied mainly by a single intercostal nerve, which shows no indication of a plexus dorsally, but which is joined with the nerves directly anterior and posterior to it by small anastomoses directly before it enters the fin.

As regards the complex pectoral arch (*cf.* 29) I have no remarks to offer, but must refer briefly to Wiedersheim's recent researches on the vertebrate pelvis.† In form the cartilaginous pelvis of Protopterus most nearly resembles that of Menobranchus, except that it does not reach the vertebral column, as is also the case in Proteus and Amphiuma, and, as in them, may be taken to represent the ischiatic and pubic regions, with a paired prepubic process extending dorsally in an intermuscular septum and a median ventral beak-like epipubis; it is quite as well developed as in these two Amphibians, and more so than in most fishes, amongst which it most nearly approaches that of Chimæra. It will thus be seen that

* For other branches of the vagus, see Pl. XVII., fig. 71, and Pl. XIV., fig. 47.

† These researches, which relate to both extremities, have since appeared in a complete and collected form ("Das Gliedmassenskelet der Wirbelthiere," &c., Jena, 1892), and contain a theory of the evolution of the limbs. *Cf.* also "Die Phylogenie der Beutelknocken" (Zeitschr. f. wiss. Zool. LIII., Suppl., 1892), by the same author, in which the pelvis of the Dipnoi is compared with that of Polypterus.—[*Note in Press.*]

degeneration has affected the free portions of the limbs only. The disposition of the pelvic arch and fin immediately in front of the vent is undoubtedly a primitive condition, which is retained in fishes only in Elasmobranchs, Sturgeons, and some Siluroids.

There can now, I think, be little doubt * that the skeleton of the fins in the Dipnoi (Ceratodus) does not represent a primitive form, or archipterygium, but on this subject I will only refer to the more recent papers of Baur, † Schneider, ‡ and Howes (8), in which the literature of the subject is given. The last-named author considers that "the paired fins of the Plagiostomes and Dipnoi have in all probability arisen independently from a type of fin most nearly represented by that of the living Chimæroids." It is usually assumed that the uniserial type seen in Protopterus has been derived from the biserial type of Ceratodus: this is very probably the case, but it is not impossible that the immediate ancestors of both forms possessed a uniserial fin, Ceratodus becoming specialized, and Protopterus, and more particularly Lepidosiren, degenerated in this respect. §

* I should, however, mention that the contrary view to that expressed above has recently been again advocated by Cope, "The Homologies of the Fins of Fishes" (Amer. Nat., 1890). *Cf.* also A. Smith Woodward ("Catalogue of Fossil Fishes in the British Museum," vol. ii., 1891, Introduction).

† "Ueb. das Archipterygium," &c.—Zool. Anz., VIII., p. 663, Jahrgang 1885.

‡ "Ueb. die Flossen der Dipnoi u. die Systematik von Lepidosiren u. Protopterus."—Zool. Anz., IX., p. 521, Jahrgang 1886; and Zool. Beiträge, Bd. II., Breslau, 1887. *Cf.* also Wiedersheim, *loc. cit.*

§ Although I quite agree with Schneider (*loc. cit.*) as to the generic distinction between Protopterus and Lepidosiren (see Summary), I cannot help thinking that he is mistaken with regard to the two species of Protopterus he describes. The form from the Gambia (*P. annectens*, Owen) is said to possess no lateral cartilaginous rays on the fins, and thirty-five ribs, while in *P. amphibius* (Peters), from Quelimane, lateral rays are present, and there are only thirty ribs. I can only state that my specimens came from the Gambia, and those which I examined for the purpose, possess, in the middle part of the fin, numerous cartilaginous parameres on each segment in both fins, and thirty-five ribs. Though I am inclined to think that Schneider may have overlooked the parameres in *P. annectens*, it is possible that there is considerable variation in both these respects within the same species.

Cf. Baur (2), who gives a list of the Bibliography as well as the specific characters of the Dipnoi. Also Giglioli ("Nature," p. 575, 1888) and Howes ("Nature," p. 583, 1888.)

Tail.

The apex of the tail presents much variation in form in different individuals. In many, it is produced into a longer or shorter filament which bends slightly upwards, giving a suggestion of a heterocercal condition, and this was particularly noticeable in many torpid specimens when they were removed from the "cocoon." In other cases the tail has a more perfectly and characteristically diphycercal form, and it is very probable that the terminal filament, like the ends of the paired fins, is often lost by accident. These facts are interesting as giving support to the view that the tail of the Dipnoi does not represent a primitive protocercal form, but that the "true caudal fin has become all but aborted like that of various Teleostei, and that the apparent caudal fin is formed by the anal and dorsal fins meeting around the end of the stump of the tail." * The facts noted by Traquair (26) show still further that it is impossible to draw any conclusions with regard to the ancestral form of caudal fin in the Dipnoi from a study of adult forms.†

Integument.

The epidermis in middle-sized specimens is, on the average, about 100 μ thick. Its internal surface is regular, except in the region of the snout, where it becomes much folded (Pls. VIII.–X., figs. 8-22).

* Balfour and Parker "On the Structure and Development of Lepidosteus."—Phil. Trans., 1882.

† It is very possible, as Mr. Howes has suggested to me, that the indication of heterocercality seen in the tails of many individuals may be present only in "restored" tails. If this should prove to be true, it is probably, like the arrangement of the scales in the reproduced tails of Gymnophthalmus and Ophisaurus amongst Lizards (see Boulanger, Proc. Zool. Soc., p. 351, 1888), to be accounted for by reversion.

The recent researches of Barfurth ("Versuche z. functionellen Anpassung."—Arch. f. Mik. Anat., Bd. XXXVII., 1891) seem, however, to indicate that no important morphological conclusions can be based on the facts described above.

The epidermic cells are arranged in several rows—about six on the average. The superficial row is somewhat flattened, each cell being provided with a cuticular cap, which is definitely transversely striated * (Pl. VIII., fig. 2; and Pl. XIII., figs. 37 and 38). The deeper cells are more irregular in form, and amongst them, here and there, smaller cells can be seen, which I take to be leucocytes (Pl. XIII., fig. 38, *leu*).†

The first point which strikes one on examining a surface view (Pl. XIII., fig. 36) or section of the epidermis is the great abundance of mucus-secreting goblet-cells (*g.c.*) which may be seen in various stages of development. So numerous are these structures that in most regions the space between any two of them is less than the diameter of a single goblet-cell: on the extremities they are less numerous. Each of these has a somewhat oval form, and occupies, when fully formed, almost the whole thickness of the epidermis, opening on to the surface of the latter by a minute aperture (Pl. VIII., fig. 2; and Pl. XIII., figs. 36-38, *g.c.*). The fully formed mucus cells are thus arranged closely packed in a single row, and between them may be seen others in an earlier stage of development which have not yet acquired their apertures to the exterior. The main body of each becomes filled with mucus, while the nucleated remains of the protoplasmic contents can often be recognised at the base.

The presence in Protopterus of multicellular integumentary glands, very similar to those of Amphibia, was noticed by Kölliker (15) in 1860.‡ He, however, gives no figure of them, and his observations on the integument of Rhinocryptis (Protopterus) appear to have been often overlooked by subsequent writers. Paulson (23) for instance, writing four years after Kölliker, makes no mention of these glands, although he figures the

* *Cf.* G. Wolff ("Die Cuticula der Wirbelthier-Epidermis."—Jenaische Zeitschrift, Bd. XXIII. N. F., 16, 1889), who considers that a striated border on the epidermis indicates the former presence of cilia. I have not observed a thin "pseudocuticula" external to the striated border, such as he describes in perennibranchiate Amphibians.

† *Cf.* J. H. List, "Ueb. Wanderzellen im Epithel."—Zool. Anz. 8, Jahrg. 1885.

‡ At the close of Kölliker's Paper it is stated that a continuation is to follow, but I have been unable to find this second part. In the new edition of his "Handbuch der Gewebelehre des Menschen," Bd. I., p. 95, 1889, Kölliker gives a figure of the goblet-cells as seen from the surface of the epidermis.

epidermic cells and unicellular glands for the first time; and I can find no allusion to them elsewhere.

These glands are most numerous on the snout (Pl. VIII., figs. 8-12, *gld.*), in some parts of which as many as twenty may be counted in a single transverse section of the entire head. On the posterior part of the head they are fewer in number (Pl. X., figs. 19 and 20), and on the body and tail their number is still further reduced, many sections of the entire animal through these regions showing none, and others not more than two or three at the most (Pl. X., figs. 21 and 22, *gld.*). They do not seem to be limited to any particular region, but occur irregularly, two or three often being seen in close proximity; they are present on the median fins, but are absent on the paired extremities.

Each gland (Pl. VIII., fig. 2, *gld.*) is flask-shaped, and consists of a rounded or oval body, which projects into the derma, and of a narrow neck. The transverse diameter of the body* is about 70 μ mm.: it contains a small lumen narrower than the thickness of the walls, and this is continued as a fine duct down the neck, so as to open on the surface of the epidermis (*gld.*). The cells of the neck are flattened, arranged in a single row round the lumen, and are directly continuous with the superficial layer of the epidermis: those of the body of the gland are more polygonal, are arranged in two or three rows, and possess large nuclei.†

Whether the nature of the secretion of these glands is different from that of the goblet-cells, and has a protective function, as in Amphibians, it is impossible to state.‡

* It should be mentioned that these details refer to the young specimen referred to on p. 110.

† Without referring to the numerous papers on the integument of the Amphibia by Leydig and others, I may mention that the form of the multicellular glands is very similar to those of the Axolotl, figured by Paulicki (Arch. f. Mik., Bd. XXIV., 1885), in which animal, however, they all apparently become closed. It would be interesting to ascertain if this condition is to be explained by the fact that the Axolotl has reverted to an aquatic mode of life, and has retained signs of its former metamorphosis in the structure of these glands. *Cf.* Weismann, "The Transformation of the Mexican Axolotl into Amblystoma": Studies in the Theory of Descent, translated by A. Meldola, London, 1882; and also J. Carrière, "Die postembryonale Entwick. der Epidermis des *Siredon pisciformis*."—Arch. f. Mik. Anat., Bd. XIV. 1885.

‡ For an account of the structure of the slime-glands and poison-glands in the toad and salamander, see W. Schultz, Arch. f. Mik. Anat., Bd. XXXIV., p. 11.

The epidermis forms a regular and continuous layer over the derma, which consists for the most part of delicate bundles of connective tissue with scattered nuclei; in its deeper part the fibres are arranged in a thick wavy bundle, and a thinner fibrous layer lies directly beneath the epidermis; while between these layers the fibres have a more irregular arrangement. In the body and tail, the overlapping scales are imbedded in this region, even the more superficial parts of them not reaching quite to the epidermis (Plate x., figs. 19-22, *sc.*). The scales* are absent over the greater part of the head and on the extremities.

Numerous blood-vessels and nerves can be seen throughout the derma, and here and there large nests of leucocytes are present, quite filling up the space between the epidermis and the deeper bundle of dermal fibres † (Pl. IX., fig. 16; and Pl. x., fig. 22, *lg. n.*).

Pigment cells, often much branched, are abundant in the integument in most regions. In the derma they are very numerous, and from thence they extend amongst the epidermic cells, even to the superficial layers (Pl. VIII., fig. 2, and Pl. XIII. figs. 37, and 38, *pg.*).‡ A large nucleus can be recognized in many of them.

Sensory Organs.

Sense-organs of the Integument.

A continuous lateral line is plainly distinguishable extending along the body and tail at the line of junction of the dorso-lateral and ventro-lateral muscles. But in spite of the differentiation of a special lateral line, the integumentary sense-organs are not limited to this region alone: although they are present at intervals all along the line, they occur irregularly in

* *Cf.* (28) and H. Klaatsch, "Zur Morphologie der Fischshuppen, u. zur Geschichte der Hartsubstanzgewebe" (2. Theil)—Morph. Jahrb., Bd. XVI. 1890.

† *Cf.* J. H. List, "Studien an Epithelien."—Anat. f. Mik. Anat., Bd. XXV. 1885.

‡ *Cf.* J. H. List, "Zur Herkunft des Pigments in der Oberhaut," Anat. Anz. IV., p. 596; and R. Bonnet, "Ueb. Eingeweidemelanose," Verhandl. Phys. Med. Gesellsch. zu Würzburg, Bd. XXIV. 1890.

various parts of the integument (*cf.* Plates VIII.–X., figs. 8-22, *sn. o.*), and thus retain a primitive arrangement.* The lateral nerve arises from the vagus directly after its exit from the skull (Pl. XVII., fig. 71, *X. lat.*), and then extends backwards close alongside the notochord, as in Selachians and Cyclostomes, sending off branches to the lateral line along the septum which separates the dorsal-lateral and ventro-lateral muscles (fig. 22).

Anteriorly, the lateral line curves downwards and divides into two main branches about half-way between the eye and the opercular slit, the dorsal branch curving over the eye, and the ventral passing to the jaw, very much as in Chimæra (Pl. XVII., fig. 70). Along these, and more particularly in the region of the snout, sensory organs are very numerous: the precise origin of the numerous nerves supplying them I have not traced: they probably arise from the trigeminal, facial and glossopharyngeal, as in fishes.†

The form of the sensory organs is essentially similar to that seen in fishes and Amphibians:‡ they are conical bodies with a slight depression in the centre superficially (Pl. XIII., figs. 37 and 38, *sn. o.*). Each organ extends through the entire thickness of the epidermis, and thus has a superficial position. The sensory cells lie in the centre, and are surrounded by supporting cells, in some of which karyokinetic figures could be seen. The nests of leucocytes referred to on p. 121 are often present close under the sensory organs.

It will thus be noticed that as regards the position, relations, and distribution of these organs, they show a primitive arrangement, quite

* *Cf.* E. Fritsch, "Ueb. d. Bau u. Bedeutung d. Kanalsystems," &c.—Sitzungsber. Berlin Akad. d. Wissensch., p. 273. 1888.

† For details as regards the arrangement of the sensory apparatus in the integument in Elasmobranchs and Amia, *cf.* S. Garman "On the Lateral Line System of the Selachia and Holocephala," Bull. Mus. Comp. Zool., vol. xvii., p. 57, 1888; and E. P. Allis (junr.), "The Anat. and Dev. of the Lateral Line System in *Amia calva*," Journ. Morph., vol. ii., p. 463, 1889. *Vide* also, Leydig, "Zur Anat. u. Physiol. d. *Chimaera monstrosa*," Müller's Archiv, 1851; and A. Smith Woodward, Proc. Zool. Soc., 1887, pp. 478 and 481.

‡ Merkel, "Endigungen der sensibeln Nerven in der Haut der Wirbelthiere." Rostock, 1880.

similar to that met with in the young stages of fishes and in aquatic Amphibians.

In young specimens the integumentary sense-organs of the head are situated in shallow grooves of the epidermis (Pl. VIII., figs. 8-12, *sn. o.*). In older specimens these grooves become deeper, and eventually give rise to definite sensory tubes lying within the derma and opening on to the surface by apertures which are plainly distinguishable by the naked eye (Pl. VIII., fig. 70, and Pl. XIII., fig. 37, *sn. t.*).* The epithelium lining these tubes is essentially similar to the rest of the epidermis, except that the goblet-cells are small and comparatively few in number.

Thus in the head the embryonic condition observable in the body is not retained: definite sensory tubes are formed, and the sense-organs lying within them are protected, as in most fishes; but the scales and bones of the skull are not perforated by the tubes, as is characteristically the case in those members of this class in which bones and imbricating scales are present.

The retention of superficial integumentary sense-organs in an animal which leads a terrestrial life during a greater part of the year is especially interesting. In the Amphibia these organs always sink down into the deeper part of the epidermis, and probably undergo degeneration during metamorphosis.

Sensory Organs of the Oral Cavity.

The character of the epithelium lining the oral cavity and pharynx and covering the tongue, is essentially similar to that of the epidermis, except that it is in many places thicker, consisting of a larger number of rows of cells with fewer goblet-cells between them: those of the superficial row are provided with cuticular caps.

The epithelium, more particularly that of the tongue, is raised up into a number of blunt, conical papillæ (Pl. VIII., fig. 3, and Pl. XI., fig. 27), which appear to be less marked in young individuals (Pl. IX., figs. 13-16). The

* *Cf.* Balfour, "Elasmobranch Fishes," and "Comp. Embryol."; and Beard, "On the Segmental Sense-organs of the Lateral Line."—Zool. Anz. VII., Jahrgang 1884.

flask-shaped sense-organs, situated on the summits of these papillae, are most numerous on the tongue and palate, and are absent on the lips. The oral epithelium thins away slightly around them, so that their bases, while not extending below the general level of the epithelium, are surrounded by the subepithelial connective tissue (Pl. VIII., fig. 3). In form they are flask-shaped, and the cells composing them are elongated, the nuclei being situated in the deep, broader part, composing the body of the flask; while the neck is formed of the narrow non-nucleated ends of the cells, which abut against the oral epithelium peripherally; the neck has often a wavy contour, and its superficial end is slightly concave. The central sensory and peripheral supporting cells composing these organs are apparently similar in form, but the nuclei of the former appear to be less coarsely granular, and to stain more deeply than those of the latter. These organs doubtless function as taste-buds. Their nerve supply I have not followed out. Ayers (1) has described somewhat similar organs on the palate of Ceratodus.*

End-buds essentially similar to those described above are found irregularly all over the body in many fishes, as well as on the lips and in the oral cavity; while in the Amphibia and all the forms above them, they are restricted to the mouth.† So far as I have been able to observe, *all* the sensory organs in connexion with the epidermis have the form of the "lateral-line organs" described above, and in this point, therefore, as in many others, Protopterus resembles Amphibians more than fishes.

Olfactory Organs.

Each olfactory organ is enclosed in a fenestrated cartilaginous capsule, external to which are two labial cartilages, an anterior and a posterior, supporting the thickened lips. It is separated from its fellow by a stout

* *Cf.* also F. E. Schulze, "Ueb. die inneren Kiemen der Batrachierlarven, I. Mittheil., Ueb. das Epithel der Lippen, der Mundrachen-u. Kiemenhöhle erwachsene Larven von *Pelobates fuscus*." Abhandl. d. König. Preuss. Acad. d. Wissenschaften. Berlin, 1888.

† *Cf.* Wiedersheim, Lehrbuch d. vergl. Anatomie, 2. Auflage, p. 364, 1886; and Allis (*loc. cit.*).

cartilaginous septum nasi, the place of which is gradually taken posteriorly by the strongly ossified palatopterygoid with its ridge-like teeth, which separates the two nasal sacs in this region. A thick fenestrated bone (the *nasal* of Huxley and Wiedersheim), which may be called the supra-ethmoid, overlies the septum nasi (Pl. VIII., figs. 9-12, and Pl. XI., fig. 26).

In its general form the olfactory organ of Protopterus comes nearest to that of Elasmobranchs, with which it has many points of similarity. It seems to resemble closely that of Ceratodus (7) and that of Lepidosiren (4, 12).

Each of these organs (Pl. XI., figs. 25 and 26) has the form of an elongated oval sac, the walls of which are raised into a number of transverse folds. These are connected together dorsally by a somewhat irregular longitudinal fold, while ventrally they fade off, so that the floor of the sac is smooth (*cf.* Owen, 20). The epithelium covering these gives rise to a number of secondary transverse folds. Thus the necessary increase in surface of the olfactory mucous membrane is effected in the same manner as in fishes and perennibranchiate Amphibians, there being no trace of a turbinal.

The presence of posterior as well as anterior nostrils, however, places the nasal organ of the Dipnoi on a higher level than that of any fish, though the resemblance to Scyllium or Raja, for instance, and still more to Chimæra or Cestracion, would be very close if one supposes that the margins of the naso-buccal grooves in these fishes were to become united, so as to give rise to an anterior nostril opening in front of the mouth, and to a posterior nostril opening behind the lips, just in front of the palatopterygoid.

The posterior nares open into the mouth at the hinder limit of the olfactory sacs, external and anterior to the palatopterygoid teeth: the anterior nostrils have a peculiar position in the Dipnoi, inasmuch as they cannot be seen when the mouth is completely closed, and thus they have sometimes been described as opening into the mouth. But as Huxley (11) has shown, this is not really the case. If the lateral overhanging lips are slightly separated from one another, the nostrils can be seen from the exterior, and their disposition is essentially Selachian. If we suppose that

a special growth of the margins of the snout, supported by the labial cartilages, has taken place anteriorly and dorsally to the external nares, and that a similar growth has occurred in the lower jaw, so as to form the thick cushion-like lips, the position of the nostrils is easily explained, and as they lie in front of the vomerine teeth (p. 130) there is no reason at all to look upon their disposition as essentially different to that seen in other Vertebrates, and their apparently anomalous position is probably to be explained, at any rate in Protopterus, as an adaptation to the habits of the animal in connexion with its summer sleep.*

The various appearances presented by the olfactory epithelium in transverse sections of the sacs (Pl. VIII., figs. 10-12, and Pl. IX., fig. 13) are to be explained by the fact that the transverse and longitudinal folds of the mucous membrane are cut through in various planes: in sections through the posterior part of the organs the epithelium thus appears like a number of closely packed tubes. There is no pigment in the epithelium, at any rate in young individuals.

I have not made a special study of the nasal epithelium, but it appears that the olfactory cells have a diffuse disposition in some parts, and in others are arranged in groups.†

As Protopterus lives out of the water for a certain part of each year, one would expect to find a glandular apparatus in connexion with the nasal organ in order to ensure the necessary moisture for the olfactory mucous membrane. No specialized glands are, however, present; but as the epithelium of the mouth, as well as that lining the anterior and posterior nasal passages, contains numerous goblet-cells, the necessary secretion is doubtless supplied by them. In correspondence with the absence of any orbital gland (*vide infra*) there is no naso-lachrymal duct.

* Ayers (1) describes the presence of "sensory (?) papillæ" in the anterior nostrils. I have seen nothing which could correspond to these.

As in all probability Protopterus can only smell substances which it has already seized in its mouth, one might compare its olfactory organ *physiologically* to a Jacobson's organ.

† *Cf.* J. Blaue, "Untersuch. ueb. d. Bau d. Nasenschliemhaut bei Fischen u. Amphibien nämentl. ueb. Endknospen als Endapparate des Nervus Olfactorius."—Archiv f. Anat. u. Physiol., 1884; and A. Dogiel, "Ueb. d. Bau d. Geruchsorgans bei Fischen u. Amphibien."—Biol. Centralblatt, Bd. VI., 1886, and Archiv f. Mik. Anat., Bd. XXIX., 1887.

The Eye.

The eye is relatively small (Pl. XVII., fig. 70, and Pl. X., figs. 14 and 15), and there are no eyelids; the pupil is round. There is no trace of a lachrymal or Harderian gland. The four recti muscles were seen by Humphry (9), but in addition to these there are two obliques, all the eye-muscles having a similar arrangement to those of fishes and Amphibians. According to Hyrtl (12) the obliques are wanting in Lepidosiren, but a further examination would probably prove their presence. The whole region between the eyeball and the orbital space which is not taken up by the eye-muscles, is filled with a delicate connective tissue, consisting of fine fibres and connective-tissue cells, enclosing lymph-spaces. A similar tissue is present around the eye in Ammocœtes,* while in adult fishes the corresponding region is filled by a gelatinous and fatty mass: this is only one of many examples of the retention of an "embryonic" character in the tissues of Protopterus.

The epidermis of the head passes directly into the conjunctiva, which it resembles in structure, except that the latter is thinner than the former, and contains fewer goblet-cells. The cornea is thick and fibrous, and is continuous at its margin with three other mesodermic structures. Directly beneath the junction of the conjunctiva with the epidermis proper, it passes into the derma; its deeper part is continuous with the sclerotic; while its middle portion, lying between these two, passes into the orbital connective tissue.

In young specimens the sclerotic is almost entirely fibrous, though small islands of cartilage become developed at the points of insertion of the eye-muscles. As development proceeds, these cartilaginous rudiments gradually extend until they replace the fibrous tissue all round the sclerotic, so that in the adult the latter is entirely cartilaginous. I am not aware whether this mode of development of the sclerotic is the usual one in other forms, but at any rate it is interesting as showing the probable

* Carrière, "Die Sehorgane der Thiere." München u. Leipzig, 1885.

manner in which the chondrification of the eye-capsule arose. As in most other parts of the cartilaginous skeleton, the large granular cells are separated from one another by a relatively large amount of the hyaline matrix.

The lens is globular, and fills up about two-thirds of the vitreous chamber. It is made up of a number of elongated fibres with large oval nuclei, while externally a well-marked epithelium can be recognised, the cells becoming more elongated and oblique peripherally, and passing gradually into the fibres just as, *e.g.*, in the Newt and Axolotl.

The choroid consists of a loose vascular network of lacunar tissue, which contains no pigment except where it is continued into the iris: * in this region a comparatively few branched pigment cells can be seen.

With the exception of these few scattered mesodermic pigment cells in the choroideal portion of the iris, the whole of the pigment of the eye is ectodermic in origin, and is formed from the outer layer of the secondary optic vesicle. The pigment epithelium of the retina consists of nucleated cells which send well-marked pigmented processes in between the elements of the rod and cone layer, as in Petromyzon (Carrière). By far the larger amount of irideal pigment is also formed from its ectodermal portion. Pigment cells are very abundant in this layer of the iris, which on its inner side is lined by a single layer of epithelial cells, continuous with the retina. The mesodermic part of the iris has a similar structure to the choroid, except that a few scattered pigment cells are present in it. There are apparently no ciliary processes, nor have I been able to distinguish any ciliary muscles; † but these muscles are difficult to recognise in the Amphibia, and one would expect that they must be present in Protopterus, as there is no *processus falciformis* or *campanula Halleri*.‡

* In my preliminary Paper (21) I stated that the iris is not present in young individuals. This mistake was due to the fact that the eyes of the specimens I had till then examined were very much shrunken. Hyrtl (12) and Bischoff (4) found no iris in Lepidosiren.

† That the pupil reacts to light has been shown in the case of Protopterus, as well as in that of fishes and Amphibians, by E. Steinach, "Untersuch. zur vergl. Physiol. der Iris."—Archiv f. d. gesam. Physiol., Bd. XLVII. 1890.

‡ A *processus falciformis* is also absent in Ceratodus (7).

The structure of the retina has been described by Schiefferdecker,* who states that its various elements, especially the nuclei, are very large, the rods and cones being similar to those of Ceratodus. He considers that the retina shows a direct transition between that of fishes and that of Amphibians. The retinal blood-vessels enter the eye along with the optic nerve, forming the *vasa hyaloidea*, which extend through the vitreous chamber up to the margin of the lens.

The structure of the auditory organ has been fully described by Retzius,† who shows that it resembles that of Selachians, most nearly approaching that of Chimæroids.

Alimentary Canal and its Appendages.

Lips and Oral Epithelium.

The lips (Pl. XI., figs. 25 and 27) are constituted by cushion-like folds of the integument, supported by the labial cartilages. When the mouth is closed, the upper lip shuts over the lower one on each side like the lid of a box (Pl. XVII., fig. 70, Pl. VIII., figs. 8-12, Pl. IX., fig. 13). The epithelium which covers them is quite similar to the epidermis: it is provided with goblet-cells, and multicellular glands are present within it, even in parts which cannot be seen externally when the mouth is shut.

The underlying connective tissue is delicate and very rich in nuclei: like so many of the tissues of Protopterus, it has an "embryonic" character. A number of strong (? elastic) fibres can be seen in transverse sections, radiating from the upper and lower labials into the lips (figs. 5-12, *f.t.*); and a gradual transition from cartilage to fibrous tissue can be observed in this region, the labial cartilages being doubtless developed where a stronger support is needed. I am unable to support Ayers's statement (1) as to the presence of muscular fibres in the lips, and thus the rule still holds good that labial muscles are confined to the Mammalia. No horny plates or

* "Studien zur vergl. Histol. der Retina."—Archiv f. Mik. Anat., Bd. XXVIII. 1886.

† "Das Gehörorgan d. Wirbelthiere," I. Stockholm, 1881.

papillæ are present on the lips, such as have been described by Ayers in Ceratodus (1), and which he compares to the horny teeth of Petromyzon (*cf.* p. 134).

The curious cushion-like folds of the mucous membrane, which extend between, and largely hide, the projecting points and ridges of the teeth (Pl. XI., figs. 25 and 27), are mentioned by several observers. The epithelium covering these is throughout much folded, so as to give rise to a number of blunt conical papillæ, on the summits of which the taste-buds already described (p. 124) are situated. In the regions between the papillæ, the epithelium is greatly thickened, so as to present the appearance, in sections looked at under a low power, of a number of close-set simple glands with rounded bases: the true integumentary glands, however, do not extend into the mouth beyond the lips,* but goblet-cells are abundant throughout the oral epithelium. The papillæ appear to be less marked in young individuals, while the epithelial folds between them are very distinct. By a further development of grooves of this kind, the cushion-like folds of the oral mucous membrane already mentioned (which extend between the projecting parts of the teeth) are produced, and the margins of these grooves nearly meet in places. In the small triangular cushion which projects backwards between the two anterior points of the mandibular teeth, a similar longitudinal groove is developed, the margins of which come into close apposition, so that it cannot be seen except in transverse sections (Pl. VIII., figs. 10 and 11, *ep. f.*), in which it has the appearance of a closed tube, connected with the epithelium, and projecting into the underlying connective tissue. The cells lining it are quite similar to those of the rest of the oral epithelium; they are provided with cuticular borders, numerous goblet-cells are present, and coagulated mucus can be seen in the lumen. In my sections of a young specimen (figs. 10 and 11), the lumen of this tube appeared to be completely closed in the greater part of its extent, but its walls were seen to be continuous with smaller folds anteriorly. From the examination of older specimens I have little doubt that

* It has recently been shown by F. E. Schulze (see p. 124) that multicellular glands are present in the pharynx of the larval Pelobates. They have a somewhat peculiar form, and do not extend below the general level of the epithelium.

this structure is not a closed tube, but simply a groove, the margins of which, at any rate in prepared specimens, are closely applied to one another, the appearance in the sections above referred to being due to shrinkage.

Tongue.

The tongue (Pl. VII., fig. 1, and Pl. XI., fig. 27, *t.*) is a large organ, firmly fixed to the floor and sides of the mouth throughout its greater part, but becoming free anteriorly, where it is produced into a small, blunt, conical process in the middle line. The free apex lies in a deep transverse hollow in the floor of the mouth just behind the mandibular teeth. The surface of the tongue is covered with numerous conical papillæ, like those of the other parts of the oral epithelium, but larger and more marked, at any rate in older individuals. Taste-buds are situated on the apices of these papillæ (*cf.* p. 124), and the character of the epithelium is quite similar to that of the rest of the mouth.

There are no intrinsic muscles in the tongue, and its anterior third consists, beneath the epithelium, entirely of delicate connective tissue, similar to that in the lips and snout (Pl. XI., fig. 27, and Pl. IX., fig. 13, *t.*) Posteriorly, a mass of extrinsic muscles constitutes the main body of the organ. These consist on either side of a large mass which is continued forwards from the ventral muscles of the trunk and inserted on to the hyoid close to its symphysis (*t. msc.*[1]), and, more externally, of a small band of muscle which, arising from the base of the first branchial arch, is also inserted on to the hyoid symphysis, dorsally to the first-named muscle (Pl. XI., fig. 27, and Pl. IX., figs. 14 and 15).

Teeth.

I have nothing to add to the description of Peters (24), Owen (20), Günther (7), and others, as to the general form and relations of the teeth. As regards their mode of fixation to the jaws, they seem to approach Chimæra more than any other living form. They consist of a curious fenestrated bony tissue (Pl. VIII., fig. 4), continuous with that of the jaws, of

dentine and of enamel, which latter covers their sharp, pointed or blade-like edges, the only parts which project above the general level of the mucous membrane. A surface view of the palate (Pl. XI., fig. 25) shows that the projecting parts of the palatopterygoid teeth form on either side a sharp transverse ridge, uniting with its fellow in the middle line, and then extending outwards and slightly backwards, so that its outer end is situated a short distance behind the posterior nostril (*p. pg.* t^2.) In front of this, lying about equidistant in the one direction between the anterior and posterior nostrils, and in the other between the olfactory sac and the middle line, a part of the same tooth gives rise to a projecting point on either side (*p. pg.* t^1.), which appears from the surface like a separate tooth, its connection with the posterior ridge being hidden by the cushion-like folds of the mucous membrane. The bases of these teeth lie between the septum nasi and the olfactory sacs (Pl. VIII., fig. 12; Pl. IX., fig. 13). A short distance in front of these anterior points, about half-way between them and the anterior nostrils, is a very small pair of teeth, situated near the middle line, which are quite unconnected with any part of the skull or jaws. Huxley speaks of these as "vomerine," and Wiedersheim (29) as "pre-maxillary teeth. The relations of these teeth show that the former interpretation is the correct one (figs. 11 and 25, *v. t.*).

In the lower jaw two transverse ridges of the mandibular teeth also project above the surface, the two being separated in the median line by a forwardly-directed fold of the mucous membrane. Anteriorly to these (*mn.* $t.^3$) can be seen *two* projecting points of the same teeth on either side (*mn. t.* $^{1 \text{ and } 2}$) instead of one, as in the upper jaw (Pl. VIII., figs. 10–12; Pl. IX., fig. 13; and Pl. XI., fig. 27).

The epithelial folds at the margins of the teeth have already been described (p. 130). Each of them passes downwards towards the base of the tooth, and is then again reflected upwards over its surface, so as to cover the apex like a cap. Some little distance below the apex, the inner cells of this layer become cornified, and the cornification gradually extending to the whole thickness of the epithelial layer, a complete horny cap is formed over the tooth (Pl. VIII., figs. 4 and 10–12, and Pl. IX., fig. 13.) In most of my preparations, however, the horn is broken away at the apex,

and in all probability the cap is never complete during the active life of the animal, for it must quickly become cut through by the underlying enamelled cutting edges. Remains of it can always be recognised, not only in wet and dry sections,* but even on the bases of the entire teeth with the naked eye: possibly it may undergo a regular renewal during the torpid period. This cap very probably corresponds to the epithelial and horny layer covering the entire enamel of unworn teeth, known as the *cuticula dentis* or "Nasmyth's membrane."†

I have not so far been successful in following out the relations of the enamel, and it is not therefore represented in fig. 4. In decalcified sections it is not visible, and in ground sections of the hard teeth it becomes so easily broken away that the determination of its relations to the rest of the tooth is by no means an easy task. What I have now to describe is therefore very incomplete, and I can only mention briefly what my sections show, and give a tentative explanation of the meaning of the appearances observed.

A short distance from the apex of the teeth, beyond the point at which cornification of the epithelium begins, the latter is seen to be differentiated into two layers (Pl. VIII., fig. 4). The outer layer (*ep.*) is continuous with the horny layer on the one hand, and the general epithelium of the mouth on the other; while the inner layer (*en.*) gradually becomes split off from the outer, and passes downwards, becoming closely applied to the bony base of the tooth, in which region its cells have a more columnar form. It appears to me that this epithelial ingrowth represents part of the "enamel organ." But in my preparations it apparently stops short at the base of the tooth, and shows no differentiation into an inner and an outer layer. With this exception, however, the relations of the epithelium, as well as of the horny cap, show a considerable resemblance to a semidiagrammatic figure of the

* I am indebted to Mr. John Storrie, Curator of the Cardiff Museum, for making some sections of the dry teeth for me.

† *Cf.* Emily Nunn, "On the Development of the enamel of the teeth of Vertebrates," Proc. Roy. Soc., vol. xxxiv., 1883—more particularly Pl. II., fig. 4, representing a longitudinal section of the spine of the Thornback.

tooth of Bdellostoma, given by Beard,* though the horny cap is much less developed in Protopterus † than in the Myxinoids.

Amongst other Vertebrates, it is now known that horny teeth and true teeth are present in Marsipobranchs and Monotremes,‡ the latter disappearing to a greater or less extent on the development of the former. There seems further to be every probability in favour of the assumption that *all* the horny structures present in connection with the mouth amongst Vertebrates (*e. g.* in larval Sturgeons and Amphibians,§ Siren, Chelonians, Birds, Whales, and Myrmecobius ‖) are secondary structures. The presence of a horny cap together with such highly developed teeth as those of Protopterus is therefore all the more remarkable; but if, as I have suggested, it should prove to correspond to the *cuticula dentis*, we may here have an indication of the manner in which the secondary horny teeth originated in many of the above cases. By a thickening of the ordinary cuticle of the teeth, developed from the "enamel cells," the condition seen in Protopterus is attained. A further stage is seen in Myxinoids, and as Beard remarks, "the fusion of the lingual teeth of the Myxinoids shows clearly how from separate horny teeth there may ultimately be a compound horny plate formed. It requires but the fusion of a number of such horny teeth in the lower, and again in the upper jaw, to produce a biting apparatus identical with that of a Chelonian."

* "The Nature of the Teeth in the Marsipobranch Fishes."—Zool. Jahrbücher (Abtheil. f. Anatomie u. Ontogenie), 1889, Taf. XXIV., fig. 7.

[Dr. Carl Röse, of Freiburg i. Br., has made a special study of the teeth of Protopterus since the above was written, and was good enough to show me some of his preparations this summer (1892). His Paper has not yet appeared.—*Note in Press.*]

† Ceratodus possesses horny structures on the lips (1), and it would be interesting to ascertain whether horn is present in connection with the teeth also.

‡ E. B. Poulton, Quart. Journ. Micros. Science, vol. xxix., 1888; and Oldfield Thomas, Proc. Roy. Soc., vol. xlvi.

§ J. Knoch, "Die Beschreibung der Reise zur Wolga," &c.—Bull. Soc. Nat. Moscow, 1871. For a recent account of the structure and development of the horny teeth in Batrachia, *cf.* Héron-Royer and Van Bambeke, "Le vestibule de la bouche chez les têtards des Batraciens anoures d'Europe," &c.—Archives de Biologie, tome 9, 1889.

‖ W. Leche, "Ueber Hornzähne bei einen Säugethier."—Anat. Anzeiger, IV. p. 449. Jahrgang, 1889.

Thyroid.

The thyroid (Pl. XI., fig. 27 and 27A, *th.*) lies below the epithelium of the tongue, at the boundary between its connective tissue and muscular portions, just above the hyoid symphysis. It is a small organ, consisting of two lobes, which are united to one another in the middle line by a narrow bridge, and are situated close to the larger mass of muscles (p. 131). On either side it tapers off, each lobe being somewhat pear-shaped, the lateral tapering portion being covered externally and dorsally by the smaller band-like lingual muscle (*cf.* Pl. IX., figs. 18 and 16, *th.*).

Sections of the thyroid show that it has the characteristic structure (Pl. XI., fig. 27A). It is made up of a number of closely-packed gland-like vesicles, each of which encloses a large lumen, and is composed of a single layer of slightly flattened cells provided with a basement membrane, the largest of which are about 200 μ in diameter. The usual colloid masses are seen within the lumina: these stain very deeply, and enclose a number of vesicular cavities, probably due to contraction of the mass. The connective tissue between the gland-vesicles contains numerous flattened nuclei, and encloses small blood vessels, which are, however, by no means abundant.

This organ probably corresponds to the structure which was mistaken by Bischoff in Lepidosiren (4) for a salivary gland, and which Hyrtl (12) described as being simply a fold of the mucous membrane.

*Thymus.**

The thymus is represented by a mass of lymphoid tissue lying dorsally and just posterior to the branchial arches, and consists on either side of an

* For the literature connected with the structure and development of the thyroid and thymus in various types, *vide* A. Dohrn, *loc. cit.*, on p. 110; P. de Meuron, "Recherches sur le développement du Thymus et de la glande thyroide," Recueil Zoologique Suisse, t. 3, No. 4, 1886; J. F. van Bemmelen, "Beiträge zur Kenntniss der Halsgegend bei Reptilien," Leiden, 1887; A. Oppel, "Beiträge zur Anat. des Proteus anguinus," Arch. f. Mik. Anat., Bd. XXXIV., 1889.

external and an internal part, separated by the muscles which pass from the skull to the pectoral arch. Its form and relations I have made out solely by means of transverse sections of a young specimen through this region (Pl. x., fig. 20, *tm.*).

The outer part, which surrounds the afferent and efferent vessels of the external gills, extends rather further forwards than the inner, which lies close against the pharynx and skull in the region of the articulation of the cranial rib: both portions extend backwards as far as the muscles of the latter. The whole thymus consists of adenoid tissue, full of leucocytes, each about 20 μ in diameter, and encloses small, scattered, rounded, granular bodies of a dark brown colour, which are about the size of the nuclei of the cells forming the substance of the organ, and which are probably only unstained and very granular nuclei.

Anatomy of the Alimentary Canal from Pharynx to Cloaca.

The general relations of the abdominal viscera have been described by previous writers (*cf.* 1, 14, 16, 18, and 24), and can therefore be passed over in a few words.

The body cavity (see Pl. VII.) is rounded off anteriorly and posteriorly. The pericardium (*per.*) projects into it in front, the peritoneum uniting with the pericardium around the middle of the latter. The lungs (*lg.*) extend dorsally along the whole length of the abdomen, and the liver (*lr.*), on the ventral side, reaches about half-way along the cœlome, the posterior end of which is plugged by the lymphoid investment of the kidneys (*k.*).

The pharynx (*ph.*), into which the gill-slits and vestibule of the lungs open (Pl. IX., fig. 18; and Pl. x., figs. 19, 20), narrows gradually to form a thin-walled tube, corresponding to the œsophagus (*œs.*) and stomach (*st.*), there being no definite line of demarcation between the two externally (Pl. XI., figs. 28 and 29). This tube extends about one-third of the way along the body cavity, enlarging slightly and gradually towards the pylorus. The intestine (*int.*) is about twice the length of the

stomach, and is somewhat spindle-shaped, tapering off posteriorly, where it communicates with the cloaca (*cl.*). The pylorus opens obliquely into its anterior end, towards the dorsal side; and, as the intestine in this region is of considerably greater diameter than the stomach, it bulges below it on the ventral side. Thence it curves upwards slightly, and then again, at about its posterior fourth, downwards; so that the whole canal is slightly S-shaped in a vertical direction, and does not run parallel to the notochord, as stated by Ayers (1).* The line of attachment of the spiral valve can be seen from the exterior, beginning at about the junction of its anterior and middle thirds, and ending a short distance in front of the cloaca.

The so-called "urinary bladder" (*cl. c.*) opens into the cloaca on the dorsal side of the intestine, between the latter and the urinary and generative ducts. In Ceratodus, the structure which apparently corresponds to this "bladder" is called by Günther (7) the "urinary cloaca," and the urinary and generative ducts are said by him to open into it. However this may be, its relations are very different from those of the bladder of Amphibians; and as regards position, it more nearly resembles the *processus digitiformis*, or rectal gland, of Elasmobranchs, except that it opens directly into the cloaca, and not into the rectum. As the homology of this sac is therefore by no means clear, I have suggested (21) the name of "cloacal cæcum" for it (p. 141).

The vent may be situated either to the right or to the left of the middle line, and, as Ayers (1) has shown, the abdominal pore of one side only is present. I was unable in any case to pass a bristle through the pore into the body-cavity, and my sections also lead me to believe that it always ends blindly, even in small individuals. And as I have been able to prove that definite generative ducts are present in the male as well as in the female, there is no longer any reason for supposing that this structure serves as a conduit for the generative products.†

* Amongst fishes the intestine takes a nearly straight course in Marsipobranchii, Holocephali, and some few Teleostei only. *Cf.* H. Leydig, "Zur Anat. u. Hist. der *Chimæra monstrosa*," Müller's Archiv, 1851; and Rolleston and W. Hatchett Jackson's "Forms of Animal Life," p. 421.

† Abdominal pores are very inconstant structures even in individual species of Selachians, and a single blind pocket is present in some species. *Cf.* Balfour, "The Urogenital Organs of

The walls of the stomach are of a light colour, and contain at most a few scattered pigment-cells, while those of the intestine are deeply pigmented; the bluish-black colour of the latter fades off gradually towards the cloaca.

In close connection with the dorsal and right side of the stomach is a large compact brownish organ (figs. 1 and 28–31, *sp.*) penetrated by a network of blood-vessels, and appearing like a thickened part of the wall of the stomach. This has been described by Peters (24) and Klein (14) as a spleen, by Hyrtl (in Lepidosiren) (12) as a *rete mirabile*, by M'Donnell (18) as a pancreas, and by Ayers (1) simply as a "lymphoid organ." It apparently also corresponds with the structures Günther has described in Ceratodus (7) as "fat-pads," but his description is not easy to follow; and Ayers's more recent account (1) is not a satisfactory one, owing probably to the imperfect preservation of the specimens examined. From a comparison of the structure of the spleen in other Vertebrates, more especially in Salamandra, I have little doubt that this organ is in reality the representative of the spleen: its position is peculiar only in so far as it is very intimately connected with the walls of the stomach, of which it appears to form a part (*cf.* pp. 147 and 148).

In my preliminary Paper (21) I supported the statements of most previous observers as to the absence of a pancreas in Protopterus. Since then, however, by more careful methods of preservation and staining, I have succeeded in proving that a large pancreas is present, which is even more completely hidden within the walls of the gut than is the spleen, and which has the further peculiarity of being of a deep black colour, owing to the abundance of pigment cells which it contains. It lies imbedded between the spleen and the stomach, around the bile duct, and extends backwards beyond the stomach into the walls of the intestine, forming the greater part of the tissue which fills up the first fold of the spiral valve. It is penetrated by fine ducts, which unite together and open into the bile-

Vertebrates," Journ. of Anat. and Physiol., vol. x., 1876; Bridge, "Pori Abdominales of Vertebrata," *Id.* vol. xiv., 1879; Turner, "On the Pori Abdominales of some Sharks," *Id.*; and M. Weber, "Die Abdominal poren d. Salmoniden, nebst Bemerk. ueb. die Geschletsorgane der Fische," Morph. Jahrb., Bd. xii., 1887.

duct just before the latter enters the intestine (Pl. XI., fig. 29; and Pl. XII., figs. 31 and 32, *pan.*, *pan. d.*).* There are no pyloric appendages.

The "brownish-black matter" on the right side of the stomach, below the mucous membrane and the "pad of fat," described by Günther in Ceratodus (7) as a spleen, may also prove on further examination to be a pancreas.

Professor Ramsay Wright, who was the first to observe the pancreas of Amia, informs me that in Ganoids the pancreas generally, if not invariably, accompanies the branches of the bile-duct, portal vein, and cœliaco-mesenteric artery, and is to some extent thus hidden away, as in Protopterus. Maccallum,† who has described this organ in several Ganoids, states that in some Siluroids also (*e. g.* Amiurus) the pancreas is completely embedded in the liver. And in Chimæra and certain other Elasmobranchs, the pancreas and spleen are closely connected by lymphoid tissue.

The liver (Pl. VII., fig. 1; and Pl. XI., figs. 28 and 29, *lr.*) is somewhat truncated at either end, and extends from close behind the pericardium, about half-way along the body cavity, ending slightly anteriorly to the first turn of the spiral valve. It is divided into an anterior and a posterior lobe by an oblique fissure along its dorso-lateral surface, in which the cœliaco-mesenteric artery runs. A large globular gall-bladder (*g. b.*) lies partially imbedded in its left border, between the anterior and posterior lobes. The common bile-duct (*b. d.*), which enters the ventral wall of the

* After my sections had shown me that this structure—which had previously been supposed to be only the lower and more deeply pigmented end of the spleen (*cf.* Ayers (1))—was an undoubted pancreas, I found a note at the end of M'Donnell's Paper (18) in which Melville states, from a dissection of a fresh specimen, that M'Donnell had not isolated the spleen from the pancreas, and that the upper part of the presumed glandular body the latter describes corresponds to a spleen, the lower to a pancreas. Professor Melville's conclusions were therefore perfectly correct, although he does not support them by any description of the ducts or of the minute structure of the organ in question.

† "The Alimentary Canal and Pancreas of Acipenser, Amia, and Lepidosteus."—Journ. of Anat. and Physiol., vol. XX. 1886. Balfour and Parker "On the Structure and Development of Lepidosteus."—Phil. Trans., pt. II. 1882. *Cf.* also Leydig, "Lehrbuch d. Histologie."

A somewhat similar arrangement of the pancreas apparently occurs in various Teleosteans. *Vide* E. Laguesse, "Pancreas intra-hépatique chez les poissons."—Comptes rendus hebdom. des Sciences de la Société de Biologie, ser. IX., tome 3. 1891.

intestine just posterior to the pylorus, is made up of three main factors: a hepatic duct from each of the two lobes of the liver, and a cystic duct entering between them. The liver abuts against the right kidney posteriorly (Pl. XIV., fig. 45).

A strong ventral,* as well as a dorsal mesentery (Pl. VII., fig. 1; and Pl. X., fig. 21, *d. m.*, *v. m.*), attaches the intestine to the body-walls. The former is incomplete, one or two fenestræ being present in its anterior part.†

The mesogastrium is much more delicate than the mesentery proper, and is also more incomplete. Peritoneal folds connect the liver with the body-wall laterally, and these, like those in relation with the stomach and urinogenital organs, give rise to a sponge-like meshwork of connective tissue, which extends throughout the cœlome between the body-walls and the viscera. The arrangement and structure of the peritoneum appears to be very similar to that seen in Lepidosiren (12) and Ceratodus (7); its visceral layer is especially thick and strong.

The mucous membrane lining the œsophagus is perfectly smooth, but may exhibit a number of longitudinal folds when contracted: when in a state of distension, these are entirely obliterated (Pl. XII., figs 30 and 31).

The pylorus is provided with a well-marked valve (Pl. XI., figs. 28 and 29, *py. v.*), projecting backwards into the dorsal side of the spacious anterior end of the intestine, which forms a chamber corresponding to the "bursa entiana" of Elasmobranchs (*b. ent.*), and extending backwards for about one-third of the whole length of the intestine: the bile duct (*b. d.*) opens into this chamber on the ventral side, close to the pyloric valve. The greater part of the pancreas is enclosed within its dorsal wall, and is in close contact with, but separated by connective tissues from, the

* A ventral mesentery is present in Lepidosteus along that part of the intestine which contains the spiral valve (Balfour and Parker, *loc. cit.*), and also in some Murænoids (Hatchett Jackson, *loc. cit.*).

† For some interesting remarks on the mesentery of Vertebrates, see a Paper by Howes, recently read before the Zoological Society, "On the Visceral Anatomy of *Hypnos subnigrum* with special reference to the Suspension of the Vertebrate Alimentary Canal."—Proc. Zool. Soc., 1890, p. 669.

spleen anteriorly, and the lymphoid tissue of the spiral valve posteriorly and internally (fig. 32, *pan. ly.*): in fact, from the position of these three organs, one might imagine that they were differentiations of a continuous band of tissue accompanying the alimentary canal (*cf.* p. 148, and note). The whole of the mucous membrane lining the bursa entiana is deeply pigmented, and is raised up into a number of oblique folds (figs. 28 and 32). The pancreas and lymphoid tissue in the dorsal wall project into its lumen, which is thus semi-lunar in transverse section. This projection is the beginning of the spiral valve, which is rendered exceedingly thick and solid by the large amount of lymphoid tissue which it contains; the main mass of this tissue is pigmented to about the same extent as the spleen, and much less so than the pancreas. Pigment is, however, especially abundant in the sub-peritoneal lymphoid tissue along the greater part of the intestine (figs. 30, 33). The spiral valve (figs. 28 and 33, *sp. v.*) makes six or seven turns round a central axis, and extends almost to the end of the intestine: the short posterior region, opening into the cloaca, in which it is absent, may be called the rectum (Pl. xv., fig. 54, *rc.*).

In a dissection of the intestine (fig. 28) the spiral valve has the appearance of a number of oblique cones, piled one on the other, and in its form and arrangement closely resembles that of Scyllium.* The size of the lumen naturally varies according to the state of distension of the gut: it may be fairly wide, or, as in my sections of a specimen taken directly out of the "cocoon," the intestinal walls may be closely pressed together (Pl. x., fig. 21).

The mucous membrane of the whole of the intestine, with the exception of that of the spiral valve, is perfectly smooth; and the pigment it contains becomes gradually less abundant posteriorly, as well as centrally, towards the axis of the valve. But the distribution of the pigment seems to vary in different individuals, and is apparently less marked in young than in older specimens.

The cloacal cæcum (p. 137) is a muscular sac, lined by an epithelium

* *Cf.* T. Jeffery Parker, "On the Intestinal Spiral Valve of the genus Raia."—Trans. Zool. Soc., vol. xi., Pl. II., fig. 5. 1880. The number of turns which the valve makes is more numerous in Scyllium than in Protopterus.

which is thrown into longitudinal folds (Pl. xv., fig. 54, *cl. c.*), and which is of a different character from that of the rest of the intestine, the cells composing it being shorter, and the goblet-cells rounder. At present it is impossible to say whether it is the actual homologue of the *processus digitiformis* of Elasmobranchs, from which it differs in opening into the cloaca instead of into the rectum, and in not having the structure of a somewhat complicated gland: these facts alone are not, however, sufficient to disprove the homology.*

A large aggregation of leucocytes can be seen between the cloaca and the epidermis; it is, therefore, highly probable that cells wander into the cloacal epithelium first, as has been observed by List in Elasmobranchs.†

* *Cf.* Günther's description of Chlamydoselache, "Challenger" Reports, Zool., vol. xxii. 1887. Howes ("On the Intestinal Canal of the Ichthyopsida, with especial reference to its Arterial Supply and the Appendix Digitiformis," Jour. Linnean Soc. Zool., vol. xxiii., p. 381) has suggested that this diverticulum in Protopterus most nearly recalls the "vesicula seminalis" of the female Chimæra described by Hyrtl (Sitzungsber. k. Akad. Vienna, Bd. xi., p. 1078, 1853), which opens close behind the anus. My study of the arteries throws no light on this point.

It is thus described by Günther (7):—"The vent (Pl. xl., figs. 1 and 2, *v.*) lies in the median line of the abdomen, and leads into a very short and rather narrow cloaca, which is subdivided into two by a projecting fold of the dorsal wall of the rectum (*r*). This fold answers also the purpose of a valve, preventing the contents of either of the cloacal divisions from entering into the other. The abdominal portion of the cloaca passes uninterruptedly into the cavity of the rectum, the dorsal portion (*u*) being a small receptacle for the urine and generative products." In fig. 2, the urinary and generative ducts are shown opening into the apex of the receptacle.

† "Studien an Epithelien."—Arch. f. Mikr. Anat., Bd. xxv. 1885.

Histology of the Œsophagus, Stomach, and Intestine, with their Appendages.

Mucous Membrane.

The stratified epithelium of the pharynx is continued down the tube which represents the œsophagus and stomach for some distance. It consists of only three or four rows of cells, and is about 50–70 μ in thickness in middle-sized specimens: the outer layer is flattened and has a cuticular border, and goblet-cells are abundant. Towards the posterior end of this tube, the epithelium gradually takes on a more columnar form, though still stratified; and, instead of the cuticular border, the outer cells bear cilia (Pl. XIII., fig. 39). Its thickness is here roughly about 150 μ. This posterior portion we may therefore take to represent the stomach proper, the œsophagus and stomach passing into one another without any sharp line of demarcation.

The epithelium lining the walls of the intestine and covering the spiral valve is also ciliated (figs. 42 and 43). In fresh specimens I have observed the cilia in active movement in both stomach and intestine in teased preparations (Pl. XVII., fig. 63); and although some of the cells thus isolated appeared to possess a striated border (fig. 63, *d. f.* and *g.*) instead of cilia, both in stained and unstained preparations, I am inclined to believe from a comparison with my sections that this appearance was due to the fact that the cilia had ceased to be active, and had become stuck together. In no sections have I been able to recognise a striated border on any of the cells, but beneath the cilia a hyaline refractive border can be made out (see also Pl. VIII., fig. 5). Goblet-cells are abundant throughout the epithelium.

Branched black pigment cells extend in amongst the epithelium in the bursa entiana, and in part, at any rate, of the intestine posterior to this region (Pl. XII., figs. 32 and 33, and Pl. XIII., figs. 42 and 43). But they become less abundant posteriorly, and may be present only in the outer

wall, and not in the region of the valve (figs. 33 and 34). They appear to be most abundant in large specimens, in which they are seen throughout the epithelium in a transverse section through the spiral valve, except perhaps, in its posterior portion.

The epithelium varies considerably in thickness (about 120–200 μ), and consists of cells of various lengths, wedged in amongst one another, and doubtless representing different stages in development (figs. 5 and 63): the nuclei are thus situated at different levels from the surface, those of the longest cells lying deepest (figs. 42 and 43). The shortest cells, as in the stomach, are very little longer than they are broad (about 50 μ).*

Between the epithelial cells here and there, as well as in the sub-epithelial lymphoid tissue, small rounded cells can be seen in sections both of the stomach and intestine, the nuclei of which are stained purple instead of blue, like the others, with picric acid and alum carmine. These I take to be wander-cells, but I have not followed out any further details about them, or ascertained whether they may pass into the lumen of the gut; they are seen, however, at various levels (figs. 39, 42, and 43, *leu.*). The nuclei of the goblet-cells are seen as flattened bodies at the lower ends of the cells.

Beneath the epithelium of the intestine is a layer of adenoid tissue consisting of a closely-packed mass of nucleated cells, each about 15–20 μ in diameter: this layer may here and there be almost as thick as the epithelium itself, but in most regions it consists of only three or four rows of cells (fig. 43, *ly. ep.*), in some few of which I have observed signs of division. This is bounded below by a delicate musculus mucosæ, consisting of from one to three rows of unstriated muscular fibres.

The oblique and permanent folds of the mucous membrane internal to the muculus mucosæ in the bursa entiana are covered by ciliated cells, the epithelium being apparently quite similar in character to that of

* In no region is the epithelial layer absent, as supposed by Ayers (1); and the connections supposed by him to exist between the underlying lymphoid tissue and the lumen of the gut in certain circular spots do not exist. The bad preservation of his material doubtless gave rise to the appearances which he describes.

the rest of the intestine, in which the surface is perfectly smooth and regular. Goblet-cells are present amongst the others.

It will thus be seen that there is no trace of specially differentiated gastric or intestinal glands, and Owen (20) was incorrect in supposing the former to be present.

Sub-mucosa.

For want of a better term I have used the term "lymphoid" or "adenoid" tissue, not only for the dense mass of cells lying between the epithelium and musculus mucosæ, but also for that tissue which forms the greater part of the sub-mucosa in Protopterus. This constitutes the larger portion of the thick intestinal walls, and the elements of which both it and the spleen are composed are so similar that I shall describe them together.* The relations of the spleen moreover so closely resemble those of the intestinal lymphoid tissue, that the former may be looked upon as a specialized lymphoid mass in connection with the anterior part of the canal.

The greater part of this tissue consists of a connective tissue meshwork, which encloses a number of large nucleated cells (about 30–40 μ in diameter) with fairly abundant protoplasm, in some of which karyokinetic figures may be seen (Pl. VIII., fig. 6; Pl. XII., figs. 30–34; Pl. XIII., figs. 40 and 43; and Pl. XVI., figs 56–58, *ly.*). Amongst these, however, both in the case of the spleen and intestinal lymphoid tissue, definite masses, irregular in the former, and more or less lenticular in the latter (where they lie close against the mucous membrane proper), are present, the structure of which more nearly resembles that of the sub-epithelial adenoid tissue, inasmuch as the nuclei are smaller and more densely packed, the cell body being relatively smaller (about 15–20 μ in diameter; figs. 7, 30–33, and 40, *ly.f.*). These may be compared to ordinary lymphoid follicles in structure, and are markedly different from the large-celled tissue, the cells of which resemble those of embryonic connective tissue.

* The lymphoid part of the investing tissue of the urinogenital organs has also a similar structure.

Stages in the division of the nuclei can also be seen here and there in these smaller cells.

Blood-vessels extend throughout the lymphoid tissue, and are particularly numerous in the spleen, where they form a meshwork from which the blood passes into the portal vein.

Amongst the ordinary cells of the large-celled tissue a number of irregular, coarsely-granular, branched cells can be seen. These appear to be amœboid migratory leucocytes: they do not take up borax carmine so readily as the others (figs. 6 and 7, *gr. c.*). In preparations preserved in corrosive sublimate, and stained with picric acid and borax carmine, irregular or rounded cells are present, which are probably of the same nature. Some of these contain highly refractive yellow granules (figs. 40 and 43, *pg.*[1]), and occasionally yellow spheres; in others, the granules are more abundant, and give the cells a deep brown colour, the nuclei then usually not being visible (*pg.*[2]) Some of the latter kind of cells are scattered, others are arranged in larger or smaller groups, the constituent parts of which are often so large as to make it appear that several cells have fused together to form them. Intermediate forms between the yellow and brown cells can be seen, and also, I believe, between the latter and the ordinary branched and deep black pigment cells (*pg.*[3]) which are abundant in most of the submucous tissue (especially in that of the bursa entiana), and which even extend into the epithelium.

I am not able to support Ayers's statement (1) that the spleen, when fresh, is seen to contain numerous fat-cells and spherical bodies of a fat-like substance. He compares the structure of this organ with that of the interrenals and adrenals of Elasmobranchs, and says that in structure they are all identical.

Muscular Coat.

The course and arrangement of the fibres in the muscular coat is by no means easy to follow out. They are disposed in exceedingly thin layers, and are unstriated.

Hyrtl (12) describes those of the stomach of Lepidosiren as consisting

of a very thin layer of transverse fibres; and Ayers states as regards this organ in Protopterus (1) that "eine deutliche Musculatur fehlt, doch sind zahlreiche spindelförmige Muskelzellen durch das ganze Submucosa zerstreut," and that in the intestine, "die Muskeln und Bindegewebsschichten sind schwach entwickelt."

As far as I have been able to make out, both the longitudinal and circular layers are represented in the stomach as well as in the intestine, but I have been unable to follow their exact course. The longitudinal layer underlying the thick peritoneum with its contained blood-vessels is very thin, and in most places is apparently composed of not more than two or three rows of spindle-shaped muscle-cells. The circular layer is rather thicker throughout, and in places (*e. g.* in the rectum and parts of the bursa entiana) reaches a considerable thickness: in most regions it is separated from the longitudinal layer by a greater or less amount of lymphoid tissue (figs. 30–34, *m.c.*). Fibres pass from it into the spiral valve, but these are so scattered amongst the lymphoid tissue, and apparently anastomose with one another to such an extent, that it is by no means easy to follow their course. In the axis of the valve, however, they unite into a more solid band, running alongside the central artery and vein.* This band (figs. 32–34, *msc.*) must be very important in peristalsis, its action being to press the turns of the valve against one another. The rest of the muscles of the gut are so rudimentary, that they alone would probably not be sufficient to drive the food along the thick-walled intestine. Probably they undergo a certain amount of degeneration during the torpid period, but my specimens had not been active long enough to determine this point.

A delicate *musculus mucosæ* can be recognised all along the alimentary tube, lying between the subepithelial adenoid tissue on the one hand, and the large lymphoid organs on the other.

Hyrtl (12) states that (in Lepidosiren) the organ which I name the spleen lies between the muscular and peritoneal coats, the position in which one would naturally expect to find it. But both in the case of the spleen and

* A somewhat similar arrangement of the muscles of the spiral valve is seen in Amia and Acipenser (Maccallum, *loc. cit.*).

pancreas, muscle fibres are present directly beneath the peritoneum which covers them, and they thus form an integral part of the wall of the gut. It appears that the longitudinal layer lies entirely outside these organs, and that they thus have a similar position to that layer of the lymphoid tissue of the intestine which lies between the circular and longitudinal muscles.*

This peculiar position of the pancreas, however, is not so surprising when one considers its mode of development from the enteric epithelium; in Protopterus it merely remains nearer its *locus nascendi* than is usually the case. If Maurer's† recent revolutionary statements as to the endodermic origin of the spleen be true, the same might be said of this organ also.

Pancreas.

The pancreas is composed of a number of glandular alveoli (Pl. XIII., fig. 41), each being about 80 μ in diameter, and consisting of somewhat spheroidal cells, with large central nuclei, which completely, or almost completely, fill the alveoli. Between the latter are numerous smaller blood vessels (*cf.* figs. 31 and 32), giving a section of the organ a spongy appearance; as well as innumerable large branched black pigment cells. Sections show the different ramifications of the duct cut across; these are lined by a single layer of columnar epithelium, the cells of which are not all equal in length (fig. 41 A), and a muscular layer is present in the larger ramifications.

The chief peculiarities of the pancreas of Protopterus are, therefore, its position within the wall of the gut, and its abundant pigment.

Concerning the histology of the liver I have no special remarks to offer.

* In this connection I might call attention to the well-known fact, that the mammalian spleen is provided with a contractile muscular coat, to which the variations in its bulk during functional activity are due. For some interesting remarks on this head, see Roy, Journ. of Physiol., vol. iii., p. 203.

† "Die erste Anlage der Milz, u. das erste Auftreten von lymphatischen Zellen bei Amphibien."—Morphol. Jahrbuch, Bd. XVI., Heft 1. 1890. (The view that the spleen and pancreas are genetically related to one another has since been supported by various observers. *Vide* C. V. Kupffer, "Ueb. d. Entwick. v. Milz u. Pankreas," Münchener Abhandl. Arbeiten a. d. Anat. Inst., Heft 36, Reihe VII. 1892.)

General Remarks on the Histology and Physiology of the Alimentary Canal—Comparison of Protopterus with other Forms.

Up to the present time no detailed account has been given of the histology of Ceratodus or of Lepidosiren, and my own observations on the structural elements of the alimentary canal of Protopterus are hardly sufficient to warrant any generalizations on the physiology of digestion in the Dipnoi. I can, therefore, only make a few tentative remarks and suggestions on this subject.

The presence of cilia all along the intestinal epithelium, although very common in Invertebrates, and more especially in Molluscs, has frequently, with few exceptions, been denied in the case of Vertebrates. Thus Schäfer* has stated that, "except, perhaps, here and there in isolated patches" (*e.g.* in the Frog),† "the result, perhaps, of arrested development, true ciliary motion does not occur in connection with the columnar cells of the intestine of Vertebrates. If cilia occur at all in the intestine of Vertebrates, they are certainly rare and exceptional." Many observations have, however, been recorded which show that the occurrence of cilia on the alimentary epithelium of Vertebrates is by no means so exceptional as the above quotation would seem to imply. Leaving Amphioxus out of the question, the whole of the alimentary tube is apparently ciliated in Ammocœtes, and cilia occur in parts of the canal in many, if not in most of the Ichthyopsida.‡

In the adult Petromyzon, the œsophagus and localized areas of the intestine are ciliated.§ Edinger‖ shows that cilia are of very general

* "On the part played by Amœboid Cells in the Process of Intestinal Absorption."—Monthly Journ. of Anat. and Hist., vol. ii. 1885.

† *Cf.* Van Thanhoffer, "Beiträge zur Fettesorption."—Pflüger's Archiv, VIII. 1874.

‡ *Cf.* Wiedersheim, Lehrbuch d. vergl. Anat., II. Aufl., 1886, p. 570; and "Ueb. d. mechan. Aufnahme d. Nahrungsmittel in d. Darmschleimhaut," Freiburger Festschrift z. 56. Versamm. d. deutschen Naturforscher u. Aertze, 1883; Schäfer (*loc. cit.*); Bronn's Klassen u. Ordnungen d. Thierreichs (Amphibia), Bd. II., 1873–8; and numerous other papers quoted in these.

§ P. Langerhans, Schwalbe's Jahresber., Bd. II. 1873.

‖ "Ueb. d. Schleimhaut d. Fischdarmes."—Arch. f. mik. Anat., Bd. XIII. 1877.

occurrence in the œsophagus and intestine of Elasmobranchs, Teleosts, and Ganoids, as well as in the pyloric appendages of the two last-named orders, but states that they are always absent in the stomach. Maccallum, however, describes the presence of cilia in the stomach of Amia,* and from his observations on Ganoids, it appears that the cilia are not restricted to irregular localized patches of the epithelium in these fishes, but occur on all the ordinary columnar cells. Trinkler † considers that the acid reaction of the gastric mucous membrane is unfavourable to the existence of cilia. Amongst the Amphibia, cilia may be present, not only in the mouth, pharynx, and œsophagus, but in parts of the intestine, and even in the stomach.‡ With the exception of the œsophagus of some reptiles, cilia have not been observed along the alimentary tract of the adult in the Sauropsida and Mammalia, but in embryos of the latter class they are at any rate present in the anterior part of the canal, and have been found in the human embryo, for instance, along the pharynx and œsophagus as far as the stomach.§

All these observations tend to show that a completely ciliated alimentary tract was possessed by primitive Vertebrates, and that the cilia have become reduced in most existing forms to a greater or less extent, being retained, as one would naturally expect, to a greater degree in lower and more ancient types than in the higher ones. It is thus interesting to find that animals like Protopterus, and Amia especially amongst the Ganoids, retain such a primitive condition as regards their alimentary epithelium.

* *Loc. cit.* Grant S. Hopkins has also recently given a description of the stomach of Amia, and mentions that the cilia extend from the beginning of the œsophagus to within about 1 cm. of the pylorus. He states that the ciliated character of the stomach of this fish was described by S. H. Gage in 1886 (Proc. Amer. Soc. of Microscopists, 13th Ann. Meeting, Detroit, Mich., 1890).

† N. Trinkler ("Ueb. d. Bau d. Magenschleimhaut."—Arch. f. mik. Anat. Bd. IV., 1885) has also found cilia in the stomach of the Pike and Perch.

‡ *Cf.* the Papers quoted above, and R. Blanchard, Zool. Anzeiger, III. Jahrgang 1880, Braun, Zool. Anzeiger, 1880; Klein, Quart. Journ. Micros. Science, vol. XX., and Amer. Monthly Micros. Journ., II., 1881; and V. Regeczy and Nagy. Arch. f. mik. Anat., Bd. XVIII., 1880.

§ Neumann, Arch. f. mik. Anat., Bd. XII., p. 570. 1870.

In the non-ciliated epithelium of Vertebrates we find the characteristic striated border on the margins of the cells. In certain of the cells of Protopterus, apart from the goblet-cells, I could observe no ciliary motion (Pl. XVII., fig. 63), and it was impossible to determine whether the cilia, after ceasing to move, had merely become stuck together, or whether this appearance was due to the presence of an ordinary striated border.* It is therefore possible that ciliated cells and cells with a striated border, may occur in Protopterus side by side, but in any case the former are by far the more numerous, and many of my sections certainly indicate that a completely ciliated border is present along the whole of the epithelium both of the stomach and intestine.

The nature of the striated border has been the subject of much investigation, the results of which are thus summarized by Foster† :—The striation of the border of an ordinary columnar epithelial cell is due to "a number of rods imbedded side by side in a substance which is sometimes of the same refractive power as the rods, in which case the whole border appears homogeneous, but which is sometimes of different refractive power, in which case the striation is distinct. The rods which are thought by some to be hyaline processes of the underlying cell-substance projecting into the above-mentioned cement-substance, are sometimes long and thin, sometimes short and thick, the whole border being in the former case narrow, in the latter broad. Under the influence of reagents, or of circumstances, the one condition may change into the other, and the change seems to be an active, not a passive process, since it will only take place so long as the cells are alive. This refractive border of the columnar cell of a villus is obviously a peculiar and presumably an important structure." Haidenhain‡ states that the rods of the striated border without doubt stand in close relation to

* Edinger (*loc. cit.*) found the same difficulty with regard to certain of the cells in the pyloric appendages of fishes. *Cf.* also note on p. 620 of Maccallum's Paper.

† Text-book of Physiology, 5th ed., pt. II., 1890; and see also O. Tornier, "Ueb. Bürstenbesätze am Drusenepithel."—Arch. f. mik. Anat., Bd. XXVII. 1886.

‡ "Beiträge z. Histologie u. Physiologie d. Dünndarmschleimhaut."—Arch. f. d. gesammte Physiol. von Pflüger, Bd. XLIII. (Supplementheft), 1888.

the protoplasm, and that they are imbedded in an intermediate substance, from which they can, under certain conditions, be drawn out. Thus they are not cuticular structures, but processes of the cell-body which are able to change their form and stretch out from the cell-body to various lengths, becoming thinner as they get longer.*

Some observers,† from the resemblance of the striated border to a mass of fused cilia, have considered that the rods really correspond to metamorphosed cilia, and as I have mentioned, it is not easy in some cases to distinguish between a striated border and cilia in which the movement has stopped. Wiedersheim even looks upon the striation as a modification of a more primitive ciliated condition. Schäfer combats this view on account of the fact that the striæ "fail to exhibit the fundamental and characteristic property of cilia, that, namely, of rhythmic contraction."

It seems to me, however, to be a difficult matter to draw a hard and fast line between the different forms of columnar epithelium. Amœboid endodermic cells are common in Invertebrates and in embryos of Vertebrates,‡ and in the latter, usually, at any rate, give rise to cells with a striated border in the adult. Ciliated cells may also throw out amœboid processes;§ and flagella, in such cases as Hydra,‖ may be extended and retracted, and are therefore not of a permanent nature. Ciliated cells, and cells with a striated border, may be present side by side. According to Chatin,¶ the auditory epithelium of Batrachians and Mammals, even over a small restricted area, may bear both auditory rods and cilia, and all intermediate stages between ordinary cells and sensory cells can be observed.

* *Cf.* also Wiedersheim (*loc. cit.*), v. Tanhoffer (*loc. cit.*), and Edinger (*loc. cit.*).

† *Vide* Wiedersheim ("Mechan. Aufnahme"), and Trinkler (*loc. cit.*) who attributes this view to Kutschin.

‡ *Cf. e.g.* Wiedersheim, "Beiträge zur Entwick. von *Proteus anguinus*."—Archiv f. mik. Anat., Bd. xxxv.

§ Wiedersheim, "Beiträge zur Entwick. von *Salamandra atra*."—Arch. f. mik. Anat., Bd. xxxvi.

‖ T. J. Parker, "On the Histology of *Hydra fusca*."—Proc. Roy. Soc., vol. xxx. 1880.

¶ "Recherches p. servir a l'hist. du noyau dans l'epith. auditif des Batrachiens." Paris, 1883 (Abstract in Ann. Sci. Nat. (6), Zool., T. 16, 1883).

All these facts indicate that epithelial cells may pass through a cycle, having different forms at different periods of their existence,* and that therefore, whether the striated border actually represents the ciliated border or not, the latter condition may pass into the former.†

An absorptive function has been claimed for the rods of the striated border, but it seems very doubtful whether they can ingest solid particles, and thus act like the pseudopodia of an amœboid cell. In animals like Protopterus, in which the whole alimentary tract is apparently ciliated, it seems unlikely that an ingestion of solid particles by the ciliated cells can occur, for so far as I am aware, no case of such an ingestion by a ciliated border has been recorded, and in ciliated Infusorians there is always a special ingestive depression, which does not exist in the ciliated cells of the Metazoa. At any rate, the cilia, like the rods, may be important in the absorption of fluids,‡ and it seems probable that they may also play a considerable part in causing the movement of food-stuffs along the canal.

This may explain the comparatively slight development of muscular tissue in the walls of the gut in Protopterus, which is apparently not sufficient to cause a marked peristaltic contraction of the stomach and thick-walled intestine. The musculature of the canal is not always strongly developed in fishes. Edinger states that it is very feeble in the stomach of Teleosts, and also that neither the circular nor the longitudinal layer is continued into the spiral valve in Elasmobranchs or Lepidosteus, although the valve § is well provided with smooth muscle-fibres (? *muscularis mucosæ*). The arrangement of the fibres in the valve of Acipenser, and more especially

* *Cf.* P. Geddes, "On the Coalescence of Amœboid Cells into Plasmodia."—Proc. Roy. Soc. Lond., 1880, and Trans. Roy. Phys. Soc. Edin., 1882. "A re-statement of the Cell Theory."—Proc. Roy. Soc. Edin., vol. xii., 1883–1884; and Geddes and Thomson, "Theory of Sex and Heredity," 1890.

† See A. Gruenhagen, "Ueb. Fettesorption in Darmepithel."—Arch. f. mik. Anat., Bd. xxix. 1887.

‡ *Cf.* R. Engelmann, "Zur Anat. u. Physiol. d. Flimmerzellen."—Pflüger's Archiv, Bd. xxiii. 1880.

§ The network of "ein eigenthümliches hellglänzendes Bindegewebe," which Edinger describes in this region in Elasmobranchs, in which he could observe no nuclei, appears to me, by a comparison with Protopterus, to represent the branching muscular bands described above.

of Amia, is apparently very similar to that found in Protopterus, and Maccallum states that "scattered so irregularly as they are through the valve, it is almost impossible to conceive that they represent excessively developed portions of the muscularis mucosæ."

Although lymphoid tissue is often present to a great extent in many Vertebrates, in no form is it apparently so largely developed as in Protopterus.

Lymphoid cells are present in the gut of Cyclostomes, and masses of such cells appear to exist in various parts of the intestinal tract of fishes.* Special aggregations of these cells in Elasmobranchs, Acipenser, and Protopterus, have a close similarity to the solitary follicles and Peyer's patches of Mammals. In Elasmobranchs there is also a large lymphoid organ imbedded in the connective tissue of the mucous membrane of the œsophagus;† and even in the Mammalia, abundant lymphoid tissue (Peyer's patches) may be present in the large as well as in the small intestine,‡ and even in the stomach.§

The abundance of these cells along the digestive tract even of the higher animals is probably to be partly accounted for by their importance in promoting absorption. Schäfer states that it is highly probable that the amœboid lymph-corpuscles are actively concerned in promoting the absorption, digestion, and transference into the blood of alimentary substances of all kinds, and whether they perform these functions directly or indirectly only, it appears possible that they may also play a part in the transformation of peptones.‖

* *Vide* Edinger and Maccallum (*loc. cit.*).

† Leydig, "Beiträge z. mik. Anat u. Entwick. d. Rochen u. Haie," 1862; and Lehrbuch d. Histol., 1857.

‡ *Vide* Dobson, Journ. Anat. and Physiol., vol. xxviii., 1884; Beddard, Proc. Zool. Soc., 1884, p. 395; and W. N. Parker, Proc. Zool. Soc. 1881.

§ Schäfer and Williams, Proc. Zool. Soc. 1876, p. 165.

‖ *Cf.* Haidenhain (*loc. cit.*); P. Stöhr, "Ueb. die Lymphknötchen des Darmes," Arch. f. mik. Anat., Bd. xxxiii.; E. Hamburger, "Beiträge zur Kenntniss d. Zellen in den Magendrüsen," Arch. f. mik. Anat., Bd. xxxiv., 1889; A. Ruffer, "On the Phagocytes of the Alimentary Canal," Quart. Journ. Micros. Science, vol. xxx., p. 491. 1890.

The small-celled tissue in the lymphoid investment of the gut and in the spleen of Protopterus, which I have compared to the solitary follicles of the higher animals, must, however, be sharply distinguished from the large-celled tissue which forms by far the greater part of this investment, and which is quite similar to that which covers the kidneys and gonads, except that in the latter position fat-cells are formed amongst it. Dr. E. Ziegler, Professor of Pathology in Freiburg, who kindly examined my sections, informed me that this tissue nearly resembles the loose connective tissue, rich in cells, which gives rise to the marrow of the bones and to the adipose tissue in the higher animals, and suggested that its great abundance, giving a sponge-like character to various parts of the body, may make the tissues more capable of imbibition.

The question as to the wandering of leucocytes has received much attention of late. It appears that whenever adenoid tissue is present directly beneath the epithelium, a normal migration of amœboid cells takes place,* the leucocytes passing through the epithelium into the lumen of the viscus; but the significance of this appears to be little understood at present. It seems, however, very probable that it is concerned with the ingestion of Bacteria.

In various regions of the alimentary canal of Protopterus, both in the stomach and intestine, small cells can be seen amongst the epithelium which have in all probability wandered from the underlying small-celled tissue. I have not found any within the lumen of the gut, but did not make a special examination for this purpose.

That there are several different kinds of leucocytes is now well known, and they have received various names, such as phagocytes, macrophages, and microphages.† Although I have not specially examined the fresh lymphatic tissue, I have been able to show that two very distinct forms of leucocytes occur in the blood of Protopterus. It has also been shown that certain of the wandering leucocytes are important agents in ingesting and

* *Vide* List, "Studien an Epithelien," Arch. f. mik. Anat., Bd. xxv., amongst other papers already quoted.

† *Vide* Ruffer (*loc. cit.*) and J. Arnold, "Ueb. Theilungsvorgänge an den Wanderzellen, ihre progressiven u. regressiven Metamorphosen."—Arch. f. mik. Anat., Bd. xxx. 1887.

getting rid of waste or harmful substances, such as red blood corpuscles and Bacteria, and that they are able to transport substances to different parts of the body, where these substances, which may become more or less changed in the process, are given up, the leucocytes themselves undergoing degeneration. The granules which may be observed in such migratory cells may thus be due to ingested matters, or in other cases are probably the result of katabolic changes within the cells themselves. The ingested substances may be got rid of at the surface, or be redeposited in the lymphatic glands and spleen, and in some cases it is possible that the leucocytes may serve to transport nutriment from one part of the body to another.*

The granular cells seen amongst the large-celled lymphoid tissue† in my sections may be of importance as conveyers of nutriment during the torpid period. On the other hand, the yellow granules seen in certain of them may be due to their containing the broken-down remains of red corpuscles.‡ Gradations could apparently be observed between the irregular cells with yellow granules, the rounded brown cells, which are mostly disposed in clusters, and the branched black pigment cells; and as the latter are found throughout the greater part of the epithelium of the intestine, it is possible that they may pass into its lumen, and may, therefore, be important excretory agents.

As, however, I have not followed up all these points in detail, I can only

* The researches of Kukenthal (see p. 134) on Worms, and of Durham (Proc. Roy. Soc., vol. xliii., 1888), and N. Wagner ("Ueb. die Rolle der Leucocyten in plastischen Processen bei den Wirbellosen," Zool. Anz., VIII. Jahrg. 1885) on Echinoderms may be mentioned as giving interesting details as to the migration of leucocytes amongst Invertebrates. A very full bibliography of recent contributions to the study of leucocytes is given by Professor E. Ziegler in a recent Paper ("Ueb. die Ursache u. das Wesen der Immunität des menschlichen Organismus gegen Infections-Krankheiten," Beiträge zur pathol. Anat. und zur Pathologie, Bd. v., 1889). The subject is too large a one to be more than referred to here; but I may mention that the prophylactic function of the spleen has been strongly advocated (*vide* Metschnikoff, "The Ancestral History of the Inflammatory Process," Quart. Journ. Micros. Science, vol. xxiv., 1884.)

† *Cf.* E. Ballowitz, "Ueb. das Vorkommen d. Ehrlich'schen granulirten Zellen (Mastzellen) bei winterschlafenden Säugethieren."—Anat. Anz., VI., Jahrgang, 1891, p. 135.

‡ *Cf.* R. Bonnet (*loc. cit.*); H. Hoyer, "Beitrag zur Kenntniss d. Lymphdrüsen," Archiv f. mik. Anat., Bd. XXXIV., 1880; W. Kukenthal, "Ueb. die Lymphzellen d. Anneliden,"

speak hesitatingly with regard to them, and merely wish to put forward a tentative explanation to account for the great abundance of lymphoid tissue in Protopterus. I would suggest that this may be due to the fact that Protopterus takes no food during many months in each year, during which period it is, so to speak, parasitic upon itself, the lymphoid tissue being probably of especial importance, not only in the formation of leucocytes and in the destruction of dying cells, but also in the processes of metabolism. Hunger is said to diminish the adenoid tissue of the gut, and to cause a movement of the wander-cells towards the epithelium. It would be interesting to ascertain whether this occurs in Protopterus.

There can be little doubt that a smooth internal surface of the alimentary canal is the primitive condition in Vertebrates, but that, owing to the necessity of an increase in the absorptive surface, longitudinal folds of the mucous membrane gradually arose. By the formation of transverse folds connecting the longitudinal ones, tubular crypts were developed, various stages in the differentiation of which can be recognized in Elasmobranchs, Ganoids, and some Teleosts, as well as during development in higher forms. The pyloric cæca of Teleosts and Ganoids are elongated crypts of the same nature, and these, like the spiral valve, the villi, and the network of folds of the mucous membrane in the intestine, may, in the first instance, be explained as arrangements for increasing the absorptive surface, though these cæca often contain a digestive ferment, and Maccallum believes them to be rudimentary structures, once actively glandular.*

Jenaische Zeitschrift, Bd. XVIII., 1885; J. H. List, "Zur Herkunft d. Pigments in d. Oberhaut," Anat. Anz., IV. Jahrg., 1889; Fr. Maas, "Zur Kenntniss d. körnigen Pigments im menschlichen Körper," Arch. f. mik. Anat., Bd. XXXIV., 1889; A. Oppel, "Ueb. Pigmentzellen d. Wirbelthierdarmes," Gesellsch. f. Morph. u. Physiol. zu München, Sitzung am 17. Dec., 1889; and "Beiträge zur Anat. d. *Proteus anguinus*," Arch. f. mik. Anat., Bd. XXXIV., 1889.

* *Cf.* Edinger (*loc. cit.*); R. Blanchard, "Sur les fonctions des appendices pyloricæ," Compt. rend. 96; Maccallum (*loc. cit.*); Wiedersheim's "Lehrbuch," and a Paper by Cattaneo, quoted on p. 867 of the same work; Stirling, Journal of Anat. and Physiol, vol. xviii.

The secretory function of the so-called intestinal glands of Mammals has been lately strongly doubted by Bizzozero ("Ueb. die Regeneration der slauchförm. Drüsen u. des Epithels des Magendarmcanals," Anat. Anzeiger, III. Jahrgang, 1888), who believes that the crypts of Lieberkühn are not glandular, but serve chiefly for the regeneration of the epithelium of the villi.

Longitudinal folds, which, however, disappear on distention, are retained in the œsophagus and rectum, while crypts are formed in the manner above described, first in the stomach and then in the small intestine.

True gastric glands appear to be present in most Elasmobranchs, Ganoids, and Teleosts, and to be most highly differentiated in the two last-named orders, although there is no differentiation into "chief cells" and "parietal cells," as in the higher Vertebrates.* It is therefore all the more remarkable that no trace of crypts can be seen in the alimentary canal of Protopterus. An increase in the absorptive surface is effected by the large spiral valve, and by the folds in the *bursa entiana*, but except in the latter region, the whole of the epithelium, both of the stomach and intestine, presents an even surface, without any outgrowths or involutions. Owing to this fact, and to my failure to find a pancreas at that time, I formerly supposed (21) that the processes of digestion in Protopterus had remained in a very primitive condition; and even although there can be little doubt that a digestive fluid, corresponding in nature to the gastric juice, is formed by the cells of the stomach, the absence of gastric glands is certain. Although one would expect a morphological and a physiological differentiation of the digestive apparatus to take place to a great extent *pari passu*, this does not seem to have been the case in Protopterus and certain fishes. As Edinger remarks with regard to the latter, it is not impossible that the whole surface of the mucous membrane is secretory.† In all probability each epithelial cell of the stomach gives rise, in its interior, to a drop of the digestive fluid, and

* Pepsin-forming glands may be present anteriorly as well as posteriorly to the stomach in Vertebrates. *Cf.*, amongst others, F. Decker, "Zur. Physiol. d. Fischdarmes," Festschrift, A. von Kölliker, seiner 70ten Geburtstags, p. 389, Leipzig, 1887; C. Gegenbaur, "Bemerk. üb. d. Vorderdarm niederer Wirbelthiere," Morph. Jahrbuch, Bd. IV.; Homburger, "Zur Verdauung der Fische," Centralblatt f. d. med. Wissenschaft, No. 31, 1877; F. W. Kruckenberg, "Versuche z. vergl. Physiol. d. Verdauung, mit besonderer Berücksichtigung d. Verhältnissen b. d. Fischen." Untersuch a. d. Physiol. Inst. d. Univ. Heidelberg, Bd. I.; Langley, "Physiol. of Pepsin-forming glands," Phil. Trans., 1881, pt. III.; Maccallum (*loc. cit.*); O. Rubeli, "Ueb. d. Œsophagus d. Menschen u. verschiedenen Hausthiere," Inaug. Dissert. Bern, 1890.

† *Cf.* Stirling, Jour. Anat. and Physiol., vol. xviii., p. 426; and Maccallum (*loc. cit.*), p. 628, In this connection the following passage from Laguesse's recent paper (*loc. cit.*), is especially

thus passes into the form of a goblet-cell, which discharges its secretion, and then degenerates, being replaced by a new cell from beneath. The same may be true of the cells lining the intestine, and this would not only explain the abundance of goblet-cells along the canal, but also the fact that the epithelium is several rows of cells deep, and not simple, as is the general rule.*

I am indebted to Professor Baumann, of Freiburg, for his kindness in having the following analysis of the contents of the gut made for me in his laboratory. The animal had been removed from the cocoon about three weeks before it was killed for the purpose:—

"Das Thier war 32 Ctm. lang, der Darm 14 Ctm.; der letztere war fast leer. Der Vorderdarm zeigte sehr schwach alkalische, fast neutrale Reaction, der Mitteldarm stark alkalische. Vorder- und Mitteldarm wurden vor einander getrennt; der Vorderdarm wurde dann zerschnitten, und die Stücke wurden mit 0·18 $^{0}/_{0}$ ^{ger} Salzsäure extrahirt. Die abfiltrirte saure Lösung wurde zu einer Flocke ansgewaschenen Fibrin gesetzt. Diese quoll nach kurzer Zeit (salzsäure Wirkung), wurde aber selbst nach 5 Stunden nicht merklich gelöst, so dass das Fehlen von Pepsin fest steht. Auch Labferment enthielt der saure Auszug nicht, wie sie nach vorsichtiger Neutralization derselben und Zusatz von Milch zeigte.

"Der Mitteldarm enthielt eine geringere Menge einer dicklichen bräunlichen Flüssigkeit: er wurde sammt seinem Inhalt zerkleinert, und mit der zehnfachen Menge Wasser extrahirt. Dieser Auszug enthält kräftiges diastatisches Ferment, da einige Tropfen derselben mit verdünnten Stärkekleister versetzt nach wenigen Minuten deutliche Zuckerreaction zeigten.

interesting:—"Chez ce poisson (Crenilabrus) non seulement il n'y a pas d'estomac, mais encore, comme l'a montré Pilliet chez le Sabre, genre voisin (Bull. de la Soc. de France, t. 10, 1885) il n'y a pas trace de glandes gastriques; anatomiquement et histologiquement, l'intestin commence immediatement en arrière des dents pharyngiennes. C'est là que débouchent côte a côte les canaux choledoque et pancreatique; le suc pancreatique et la bile sont les seuls liquides digestifs."

* *Cf.* Decker (*loc. cit.*, p. 106) and J. Paneth, "Ueb. d. secirende Zellen des Dünndarmepithels." Arch. f. mik. Anat., Bd. xxxi., 1888; and Trinkler (*loc. cit*).

Das diastatische Ferment ist nach Controlversuchung bei 40 Grad wesentlich wirksamer als be 20 Grad: der Darmsaft zeigte geringe Peptonreaction, dagegen gar keine Trypsinwirkung. Die Peptonreactionen waren nach 5 Stunden noch eben so minimal als anfangs. Flocken gut ausgewaschenen Fibrins wurden bei Zimmertemperatur oder bei 40 Grad mit dem Darmauszug in Berührung bleibend, nicht merkbar gelöst.

"Der Darminhalt war geruchlos; der grössere Theil des mit Wasser behandelten Darmes nebst Inhalt wurden auf Fäulnissstoffe die aus Eiweiss gebildet werden, untersucht, indem er mit einigen Tropfen Schwefelsäure versetzt und destillirt wurde. Das Destillat enthielt weder Phenole noch Indole noch Scatol: der Destillationsrückstand wurde nach dem Erkalten mit Aether extrahirt, der Aetherauszug verdünnstet, der Rückstand in Wasser gelöst und filtrirt. Die erhaltene wässerige Gelösung gab mit Millon's Reaction keine Rotfärbung. Eiweissfäulnissproducte waren im Darm nicht enthalten.

"Die prallgespannte Gallenblase enthielt wenige Tropfen einer dünnflüssigen schwachgelben mucinlosen klaren Flüssigkeit, von alkalischer Reaction. Dieselbe wurde mit 15 Cb. Ctm. Wasser verdünnt. Ein Tropfen dieser Lösung gab die Pettenkofer'sche Gallensäurereaction sehr schön. Die Lösung der Galle zeigt deutliche saccharificirende Wirkung auf Stärkekleister: die Galle enthielt also ein diastatisches Ferment, das jedoch wesentlich weniger kräftig wirkt, als das aus dem Darm.

"Die Leber enthielt wesentliche Menge von Glycogen, welche nach dem Brücke'schen Verfahren ausgezogen wurden. Aus der Hälfte (5 Grm.) der Leber könnte wenigstens 1 Decigr. reines Glycogen dargestellt werden, das alle characteristischen Reactionen zeigte. Auch die Leber enthielt ein diastatiches Ferment, welches das in ihr enthaltene Glycogen bei Zimmertemperatur allmälig in Zucker umwandelt. Dieses Ferment ist gleichfalls weniger kräftig, als das des Darmes.

"Die Muskeln enthielten so gut wie gar keine Glycogen."

It is to be regretted that the animal had not made a good meal before being examined, for the above analysis gives results incomplete as regards the digestion of animal food, and throws no light on the digestive

action of the stomach. But there can be no doubt that a peptic reaction must take place anteriorly to the entrance of the bile duct,* and it is probable that glycogen becomes stored up in the liver during the torpid period, as in the frog.

Ayers (1) also gives an analysis of the contents of the alimentary canal by Professor Baumann, but only negative results were obtained, and no digestive reaction at all could be observed. This may have been due to the fact that the specimen had lain in alcohol for a considerable time.

Respiratory Organs.

Gills.

The branchial apparatus in Protopterus is markedly reduced. The well-developed hyoid is followed by five rudimentary branchial arches,† and is supported by delicate unsegmented rods of cartilage, decreasing in size from before backwards, the fourth and fifth being connected with one another ventrally, but those of either side being independent.

The hyobranchial cleft is the smallest, and the first branchial cleft the largest, the following three undergoing a gradual reduction in correspondence with the arches.

The gill-bearing slits are protected by papillæ (gill-rakers) of the mucous membrane.

The position of the internal branchial clefts is seen in Pl. VII., fig. 1.

Sections through the branchial apparatus are figured on Pl. IX., figs. 17 and 18, and Pl. X., figs. 19 and 20. An external view, showing the operculum (2) is given in Pl. XVII., fig. 70.

* *Cf.* Gegenbaur (*loc. cit.*).

† Owen (20), Peters (14), M'Donnell (18), and Wiedersheim (29), describe *six* branchial arches in Protopterus. Wiedersheim's figure (Taf. II., fig. 8, which is copied in his "Lehrbuch" and "Grundriss d. vergl. Anat.") would be perfectly correct if the first arch were struck out, for that which he figures as the second is, I believe, in reality the first, the hyobranchial cleft lying directly in front of it. (*Cf.* Boas (5), as well as Baur (2) and Schneider (*loc cit.*)).

The arrangement of the leaf-like branchial lamellæ is as follows:—

Hyoid arch.*—A single small row, constituting a posterior hyoid hemibranch ('opercular gill').

1st Branchial arch.—Branchial lamellæ absent.

2nd ,, —Branchial lamellæ absent.

3rd ,, —A double row.

4th ,, —A double row.

5th ,, —A single anterior row, continuous dorsally with the posterior hemibranch of the fourth arch, and probably representing a special growth ('emigrants') of the latter (*cf.* Boas (5)).

Thus in the hyobranchial cleft there is an anterior hemibranch only; the first branchial cleft is without gill-lamellæ; the second has a posterior hemibranch; and the third and fourth both anterior and posterior hemibranchs, the last two being continuous over the fourth branchial cleft. There is no cleft behind the fifth arch.

In Lepidosiren there are only four slits, the hyobranchial cleft apparently becoming closed. In other points Bischoff's description of Lepidosiren (4) corresponds with that given above of Protopterus, but Hyrtl (12) states that in the former animal gill filaments are absent on the first and last arch, the latter (fifth) bearing only a pair of 'fadenförmigen Zotchen,' and the second having only a posterior hemibranch. Comparing this with the arrangement of the blood-vessels, it appears that a further reduction of the branchial apparatus has taken place in Lepidosiren than in Protopterus, though the extent of this reduction (if Bischoff and Hyrtl are both correct) may vary.

In Ceratodus, on the other hand, the structure of the gills indicates that it has not become so much modified for life out of the water as is the case in the other two genera. Besides the hyoidean hemibranch, the four anterior branchial arches bear complete gills, while no branchial lamellæ are found on the fifth. But as these latter in Protopterus are probably

* There is apparently no remnant of the hyomandibular cleft such as has been described by Ramsay Wright in Amia and Lepidosteus (Journ. of Anat. and Physiol., vol. xix., 1885).

only emigrants from the fourth arch, Ceratodus can hardly be said to have undergone a reduction in this respect.

Three pairs of external gills were present in all specimens, even the largest, which I examined, and Peters (24) found them on examples one or two feet in length: he states that in young specimens they are thinner, in older ones broader. According to Ayers (1), however, they may be absent, as they are in Lepidosiren (see also Owen (20) and M'Donnell (18)). However this may be, Ayers is certainly incorrect in saying that they are only present in young animals. In all cases they are certainly rudimentary structures, and a certain amount of variation in them would not therefore be surprising. Each consists of a filamentous stem without lateral branches, the third always being the smallest (fig. 70). They are situated directly above the operculum, in a row one above the other, and the pectoral fin arises close below them. Each consists simply of an epidermic outgrowth with a pigmented mesodermic core in which the afferent and efferent vessels run.

Lungs.

The glottis is a slit-like aperture in the median line of the floor of the pharynx (Pl. VII., fig. 1, and Pl. XIV., figs. 46 and 47, *gl.*), provided with muscles which are very probably derivatives of the branchial series. Its walls are strengthened by a fibro-cartilage * which lies directly beneath the epithelium, and extends forwards some distance anterior to the glottis (*vide* also Pl. X., fig. 20, *gl. c.*), which opens into a vestibule (*vb.*) lined by an epithelium similar to that of the pharynx, its walls not being strengthened by any skeletal structures. The vestibule passes to the right side of the œsophagus so as to open dorsally to the latter into the unpaired anterior end of the lung (*lg.*). It will thus be seen that the vestibule more nearly resembles the "pneumatic duct" of Ganoids than the more highly differentiated laryngo-tracheal chamber of Amphibians, the supporting

* This has been compared by Howes to an epiglottis ("On a hitherto Unrecognised Feature in the Larynx of the Anurous Amphibia."—Proc. Zool. Soc., 1887, p. 491.).

cartilages in which doubtless arose in connection with the development of vocal cords, which are absent in Protopterus.

The short unpaired anterior end of the lungs soon bifurcates, so that these organs are paired along almost their whole length. They are, however, in close apposition in the middle line as far back as the point of bifurcation of the ventral pulmonary artery (fig. 46), up to which point they are united by connective tissue. They extend along the whole length of the cœlome, directly beneath the notochord, gradually tapering off posteriorly.

The lungs are delicate hollow sacs, not unlike those of snakes; their internal walls are raised up into an irregular network of trabeculæ. In the paired portion, these trabeculæ only project a short distance into the central lumen (Pl. x., fig. 21, *lg.*), while anteriorly, in the unpaired region, the trabeculæ extend further inwards and anastomose with one another, so as to form a sponge-like meshwork in which a definite central lumen can no longer be recognized. In this respect the lungs of Protopterus are more highly differentiated than those of the Amphibia. Their walls become gradually thinner posteriorly.

The epithelial lining of the lungs consists of a single layer of somewhat flattened cells, with which the network of blood-vessels in the underlying connective tissue comes into close relation. Masses of smooth muscle fibres and numerous pigment cells are present in the connective tissue.*

* In my sections of a young specimen, already referred to, I noticed (21) certain appearances in the lungs which I have been unable to confirm by other preparations, but which may be briefly mentioned. It should be noted that this specimen was preserved directly after being taken out of the "cocoon." On the ventral side of the lungs, at the junction of their paired and unpaired portions, just above the liver, a specially dense mass of connective tissue could be seen, which inclosed numerous cells, having somewhat the appearance of those of the lymphoid tissue found in other parts of the body. These cells were probably migratory leucocytes. They stained deeply, and some of them could be seen penetrating the pulmonary epithelium. This probably indicates that there is a migration of leucocytes similar to that which occurs in all Vertebrates which have been specially examined for this purpose, and that they are concerned in protecting the entrance into the body of harmful substances which would pass in along with the respiratory current. And in some of them numerous small bodies could be seen which appeared not unlike Bacteria. In these sections also, numerous leucocytes, as well as red corpuscles, were observed in the meshes of the lung, that is, within its sponge-like lumen. But this was probably due to a bleeding of

There can be no doubt that the respiratory function of the lungs is very important during the active as well as the torpid condition, the gills alone probably being insufficient for the aeration of the blood.

The relations of the pulmonary branches of the vagus, as well as of the pulmonary arteries, seem to indicate that a twisting of these organs has taken place in the course of development, as they grow from their point of origin on the ventral side to the dorsal side of the alimentary tract. Close to its exit from the skull, each vagus gives off a nerve (Pl. XVII., fig. 71, *X pul.*) which passes backwards and medianwards, so that on reaching the dorsal side of the proximal end of the lung it crosses its fellow, and then runs backwards along the dorso-lateral surface of the lung of the other side (Pl. XIV., fig. 47, *X pul.*). Thus the right lung is supplied by the left pulmonary nerve, and *vice versa*, and this would seem to show that a twisting has taken place through an arc corresponding to a semicircle. On the other hand, the relations of the pulmonary arteries only indicate a rotation to the extent of 45°. Very possibly, however, this pulmonary "chiasma" of Protopterus may have another explanation, for a crossing of other cranial nerves has been observed by several anatomists.*

Concerning the "cranial rib"† and its powerful muscles, I would suggest that it very probably may be concerned with the mechanism of

the vessels, for the animal was cut into pieces before being preserved; or it may have been caused by acute inflammation, for it is known that in such pathological conditions red as well as white corpuscles pass out through the capillaries.

* A. Schneider (Beiträge zur vergl. Anat. u. Entwick. d. Wirbelthiere, Berlin, 1879) quotes several such instances. Thus C. E. Bach observed an occasional anastomosis of the right and left hypoglossal at the root of the tongue in man; Jöh. Müller states that a connection exists between a right and left branch of the trigeminal supplying the posterior part of the tongue in *Bdellostoma fosteri:* Jeffries Wyman has described a ventral chiasma of the hypoglossal in the goose and ostrich, and of the laryngeal nerve in the goose, alligator and python: and finally, Schneider himself found an anastomosis between a right and left branch of the ramus inframaxillaris in bony fishes. Schneider mentions all these cases to support the theory of the presence of an œsophageal nerve-ring in Vertebrates.

† I have little doubt that this structure really corresponds to an enlarged first rib, belonging to that portion of the vertebral axis which has become fused with the skull (*cf.* 10, 29, and other works on the skeleton of the Dipnoi). It lies in the somatopleure, and its muscles are supplied from the brachial plexus, mainly, if not entirely, from the hypoglossal.

respiration, the muscles serving to move the rib so as to alternately compress and expand the pharynx, and thus force air in and out of the glottis. But a more careful dissection and examination of these parts than I have made is necessary to settle this point. Hyrtl (12) supposes that these muscles have to do with deglutition.

In his description of the lungs of Lepidosiren, Hyrtl (12) states that the glottis is situated rather to the right of the middle line, and mentions that it is so figured, though not described, by Bischoff (4) and Owen (20—in Protopterus); the same is said to be the case in Ceratodus (7). In all specimens of Protopterus I have examined, it is certainly median (*cf.* also 18); but the above-mentioned observations indicate that there may be some variation in this respect amongst the Dipnoi. In the case of fishes, the position of the aperture of the pneumatic duct in the pharynx is not constant: though nearly always dorsal, it may be ventral (Polypterus and some Plectognathi),* or lateral (Erythrinus),† and may become shifted far backwards. These facts are interesting, as indicating the comparatively slight morphological importance of the position of the aperture by which the lungs or air-bladder communicate with the throat, even though, in cases in which the development has been studied, the former have a dorsal, and the latter a ventral origin; and it seems to me that this difference in position does not furnish any sound argument against the supposed homology of the air-bladder and lungs. Moreover, although the lungs are usually said to be paired in their origin, the outgrowth which forms them, although bifurcating close to its origin, is, in fact, so far as I can gather, *unpaired* quite at the first.‡ In the Dipnoi, at any rate, it is probable that the pulmonary diverticulum is ventral and unpaired, although it becomes paired posteriorly in Protopterus and Lepidosiren. The special blood supply of these organs is probably a secondary character—a pulmonary artery arising in those cases in which the sac becomes more definitely respiratory in function.

* See Rolleston and Hatchett Jackson's Forms of Animal Life, p. 424. Oxford, 1888.

† Hyrtl, on the authority of Müller.

‡ *Cf.* fig. 62, p. 177, in Foster and Balfour's Elements of Embryology, 2nd ed., and fig. 204, p. 252, in Wiedersheim's Comp. Anat. of Vertebrates (English edition).

It seems to me, therefore, that the air-bladder of fishes and the lungs of Dipnoans and higher Vertebrates are homologous structures, in so far as they both arise as a diverticulum from the pharynx, which may take on a purely hydrostatic function, or which may become more or less important in respiration, and finally may take on this function exclusively.*

Vascular System.

Blood.

Like most of the other histological elements of Protopterus, the blood corpuscles are exceptionally large. Peters (24), although he mentions nothing about the colourless cells, briefly describes the red corpuscles, and

* For a different view, *cf.* P. Albrecht, "Sur la non-homologie des poumons des Vertébrés avec la vessie natatoire des poissons," Bruxelles, 1886; and J. Beard, "The Interrelationship of the Icthyopsida."—Anat. Anz., v. Jahrg. 1890, p. 179. Beard denies the existence of the rudiment of an air-bladder in certain sharks, as described by Miklucho-Maclay (Jenaische Zeitschrift, Bd. III., 1867).

That the air-bladder may have an importance in the oxygenation of the blood is, I think, clearly shown by such observations as those of Poey ("Observations on different points of the Natural History of the Island of Cuba, with reference to the Icthyology of the United States."—Ann. Lyc. Nat. Hist., New York, pp. 133–137 vol. vi., 1858), and Wilder ("Notes on the North American Ganoids, Lepidosteus, Acipenser, and Polyodon," Proc. Amer. Assoc. Adv. Sci., vol. xxiv., B, Detroit Meeting, 1876, pp. 151–196, and "Gar-pikes, young and old," Pop. Sci. Monthly, vol. xi., Nos. 61 and 62, 1877, pp. 1–12 and 186–195), with regard to the habits of Lepidosteus and Amia, and by the structure of the lung-like air-bladder of the former (*vide* Balfour and Parker, Phil. Trans., part II., 1882). More recently, the analyses made by Mark, ("Studies on Lepidosteus," Part I., Bulletin of the Museum of Comp. Zool. at Harvard College, vol. xix., No. 1, 1890), of the gas emitted by the gar-pike, still further prove that the air-bladder has a respiratory function in this fish; though he obtained only negative results with regard to the elimination of carbon dioxide, he was able to prove the absorption of oxygen. *Cf.* also Semper, "The Natural Conditions of Existence as they affect Animal Life," Internat. Sci. Series, 1890, pp. 188, *et seq.*; and F. Day "On the Air-bladders of Fish," Zoologist, March, 1880; and concerning the physiology of the air-bladder of fishes, Traube-Mengarini, Arch. f. Anat. und Physiol., Physiol. Abtheil., p. 54, 1889; Morris, Proc. Philad. Acad., p. 124, 1885; and Meek, Bull. Mus. Comp. Zool., Feb., 1890.

states that they are eight times larger than those of man,* while Gulliver† gives their size as $\frac{1}{570}$ in. × $\frac{1}{941}$ in.

The red corpuscles are oval (Pl. XIV., fig. 48 C, and Pl. XVII., fig. 64 A, B), and the oval nucleus under a high power shows a distinct nuclear network. In the longer diameter each measures from 40 to 46 μ, and in the shorter diameter 25 to 27 μ. Thus they are only exceeded in size by those of certain Urodeles.‡

It is well known that the proportion of white to red corpuscles in man varies very much at different times, the average in health being probably from 1 in 300 to 1 in 700 (Foster); under certain pathological conditions, however, the proportion of leucocytes may apparently increase very greatly. In order to arrive at any accurate conclusions on this head with regard to Protopterus § it would be necessary to make calculations from specimens of blood taken from various parts of the body, and from different individuals, in both the torpid and the active condition, as well as after a meal, and when hungry. This, unfortunately, I was unable to do, the time during which I had fresh material at my disposal being too short for the purpose. All I can therefore state is, that in the specimens of blood I examined, which were taken from animals shortly after their removal from the cocoon, the relative proportion of white to red corpuscles was very large. On one slide I counted in the field of the microscope 22 white and 80 red, on another 12 white and 28 red. The average between these two gives, roughly, 1 white corpuscle to 3 red ones. But although this is probably considerably above the true average, it shows at any rate that the proportion of leucocytes is extremely large in the blood of Protopterus, and is very probably greater than in any other Vertebrate except under pathological conditions.

The size of the white corpuscles is very varied, the largest being considerably larger than the red. They retain their vitality and power of

* M'Donnell (18) also describes and figures the red corpuscles, and compares their size with those of the frog and haddock.

† Gulliver, Proc. Zool. Soc. 1875, p. 480.

‡ *Cf.* Kölliker's "Gewebelehre," 5. Aufl., 1867, Vaillant, and Gulliver (*loc. cit.*).

§ Stuhlmann believes that the proportion of white corpuscles in Protopterus is greater in the torpid than in the active state.

amœboid movement on an ordinary slide for some hours if a little oil is run round the cover glass to prevent evaporation. They are thus admirably adapted for examination in the living condition.

The fact that the white corpuscles of the blood are not all alike is now well known in the case of most Vertebrates, although it is not possible, in most cases at any rate, to state definitely whether these do or do not correspond to stages in development of one and the same thing, and whether different functions are performed by these different kinds of leucocytes. Leydig* described different forms of white corpuscles in the blood of Selachians and Amphibians, and many details on this subject have been given by subsequent observers. Thus, referring to only one or two of the more recent observations in this field, Arnold † describes in the blood of the frog, besides the ordinary finely-granulated cells, "grobgranulirter Zellen," as well as multinucleate "Riesenzellen," with finer and thicker processes. And Paul Meyer‡ shows that "Körnchenzellen" as well as ordinary leucocytes, are present in the blood of Selachians, the former of which do not exhibit amœboid movements, and probably take part in digestion. In man also, "finely granular" and "coarsely granular" leucocytes are present in the blood (*cf.* Foster); in cases of leucæmia a larger and a smaller variety can be distinguished, and in different cases either one or the other form may be the more abundant,§ the larger being supposed by Virchow to arise from the spleen, the smaller from the lymphatic glands.

Ehrlich‖ has shown that a whole series of forms can be recognized amongst the leucocytes of the blood by various staining methods: one form contains a single ovoid nucleus which stains feebly, and another possesses

* Lehrbuch d. Histologie, Frankfurt, 1857; and Untersuch üb. Fische u. Reptilien, Berlin, 1853.

† *Loc. cit.*, and "Ueb. Kern- u. Kerntheilungen in den Zellen des Knochenmarkes."—Virchow's Archiv, Bd. xc., xciii., xcvii., and xcviii. 1883, 1884.

‡ "Ueb. Eigenthümlichkeiten in d. Kreislaufsorganen d. Selachier."—Mittheil. a. d. zool. Stat. zu Neapel, Bd. viii. 1888. *Cf.* also Hoyer, Ruffer, and others.

§ *Cf.* E. Ziegler, A Text-book of Pathological Anatomy and Pathogenesis, translated and edited by D. Macalister, pt. ii. London, 1884.

‖ Verhandl. d. physiol. Gesellsch. zu Berlin, xx., 1878, 1879; and Zeitschr. f. klin. Med. i.

one or more deeply staining nuclei. The arrangement of the granules in the cell-body, and their power of taking up stains, also varies in different instances, some cells being "eosinophilous." Ehrlich further noticed that in all acute cases of leucocytosis the mono- and poly-nuclear cells increase in number, but the eosinophilous cells do not, while in other cases, as in leucæmia, the number of eosinophilous cells is increased. Thus it is certain, not only that different kinds of leucocytes exist, but that their relative proportions in the body at different times may vary; and it is more than probable that they have different functions to perform.

In Protopterus two kinds of white corpuscles can easily be distinguished, and these I will designate as Forms A and B.

Form A (Pl. XVII., fig. 65). These are large amœboid mononucleated cells, which creep about on the slide by the aid of broad pseudopodia of the ordinary form. When extended, the larger ones are considerably larger than the red corpuscles. Usually a clear ectoplasm is plainly distinguishable from the coarsely granular endoplasm, and the nucleus contains one or more distinct nucleoli. The extension of the pseudopodia takes place just as in an ordinary Amœba, the clear ectoplasm being protruded first, and the granular endoplasm then streaming into the process thus formed.

Form B (Pl. XVII., fig. 66). These vary in size more than is the case with Form A, and even the largest do not usually attain the size of the largest of the latter. No distinction between ecto- and endoplasm can be noticed, the whole cell-body being finely granular. Not only can the cell as a whole change its form, but it can also give rise to numerous fine radiating processes, something like those of a Radiolarian. The whole cell has then an appearance somewhat similar to that of the amœboid connective tissue cells described by Poljakoff* and Rabl-Rückard,† except that the pseudopodia are finer in Protopterus. The nucleus is sometimes entire, and rounded or oval in shape (A), but in most cases it is seen to have undergone some alteration, whereby various curious and irregular forms

* "Ueb. eine neue Art v. fettbildenen Organen im lockern Bindegewebe."—Arch. f. mik. Anat., Bd. XXXIII. 1888.

† "Fettzellen von eigenthüml. Form."—Arch. f. mik. Anat., Bd. XXXIII. 1888.

are produced (B–G). In some of the smaller cells the nucleus fills up almost the whole of the cell-body, only a thin peripheral layer of protoplasm remaining, which may, however, just as in the larger cells, give rise to filamentous pseudopodia (H, I).

After treatment with absolute alcohol, the protoplasm in Form A appears delicately striated, while in that of Form B no striations can be seen. Osmic acid renders the structure described above even more distinct than in the living cells.

In some cases the appearances presented by the nuclei of Form B may be due to a simple cell division, but in most instances they certainly appear to indicate a regressive metamorphosis, in which process the nucleus is first affected, and the protoplasm then becomes gradually reduced, until finally nothing but the greatly altered nucleus is left. I have observed no similar phenomena in Form A. These appearances closely resemble those described and figured by Arnold in the case of the wander-cells of the frog, as well as those noted by other observers already referred to.*

In the Protozoa similar degenerative processes are met with, as I am informed by Professor A. Gruber,† who was good enough to make a careful examination of the blood of Protopterus with me, and to whom I am mainly indebted for the above explanation, as well as for several figures of the leucocytes on Pl. XVII.

Treatment of the corpuscles by Ehrlich's method not only brings out the difference between the two kinds of leucocytes very distinctly, but also indicates still further that the phenomena observable in Form B, and in this form only, are due to katabolic changes. I am indebted to Dr. Goldmann of Freiburg for making some preparations of the corpuscles for me by this method,‡ which show the following results. In Form A

* *Cf.*, also Löwit, "Ueb. Neubildung u. Zerfall weisser Blutkörper," Sitzungsberichte d. K. Acad. d. Wissenschaft. zu Wien, Bd. XCII., 1885 ; and Pl. XX. in Norris's "Physiol. and Pathol. of the Blood," London, 1882, in which, however, the appearances figured are said to be stages in progressive development, and not in degeneration.

† "Der Conjugationsprocess bei *Paramœcium aurelia*."—Berichte d. naturforsch. Gesellschaft zur Freiburg i. B., Bd. II., 1887.

‡ A drop of blood was dried on a cover-slip and placed in an oven kept at a temperature of 120° C. for one hour. The cover glass was then floated on the staining fluid (see below) for a

(Pl. XIV., fig. 48 A) the protoplasm appears uniformly violet, and the nucleus blue, while in Form B (fig. 48 B) the protoplasm becomes reddish-brown in colour, the nucleus, however, being blue in this case also.* Dr. Goldmann informs me that a similar effect is produced by this method in the case of leucæmic human blood, the granules in the white corpuscles having a strong affinity for acid-aniline dyes, and becoming coloured just like Form B in Protopterus.

It is not improbable that the blood-cells of Form B, like the "Körnchenzellen" of Selachians, are very active agents in digestion. The question of the part played by leucocytes in this process I have already referred to, and will only mention here that I have observed no cells similar to Form B outside the blood vessels, unless the granular wander-cells amongst the lymphoid tissue and the leucocytes in the lungs, mentioned above, correspond to these. In my preparations, however, the former appear to resemble Form A more than Form B, though a further examination of fresh as well as of preserved material, treated by different methods, is necessary before anything definite can be stated on this point.

Blood Vessels.†

The details of the vascular system of Protopterus are exceedingly difficult to follow out, and although I have been able to elucidate a number

few minutes, and then dried on blotting paper; the preparation was cleared with xylol, dried again, and then mounted in Canada balsam. The stain used has the following composition:—

100	c.c.	saturated solution of		Methyl-green.
,,	,,	,,	,,	Rubin.
,,	,,	,,	,,	Orange G.
50	,,	alcohol of 96 per cent.		

* Comp. Hoyer (*loc. cit.*), Pl. XII., fig. 3. Even in my serial sections a marked difference can be seen in the staining of the white corpuscles within the vessels.

† As regards the heart, I have nothing to add to the observations of previous observers (5, 17, and 24, and for the other genera of Dipnoi, 4, 5, 7, and 12; *cf.* also Pl. VII., fig. 1, and Pl. X., figs. 19 and 20). Quite recently the structure of the heart has been described by C. Röse ("Beiträge zur vergl. Anat. des Herzens der Wirbelthiere," Morph. Jahrb. Bd. XVI., 1890, p. 27). There can be little doubt that the heart of Protopterus is more specially modified in connection with pulmonary respiration than that of Ceratodus.

of points with regard to the origin and distribution of many of the arteries and veins, I have not succeeded in making out satisfactorily the details of the blood supply to several parts: the whole vascular system will well repay further investigation. Not only are most of the obtainable specimens rather small for the purpose, rendering injection a very difficult operation, but many of the vessels are so much obscured by the abundant connective and lymphoid tissue, that a satisfactory dissection of them is far from easy. A number of the chief vessels can be injected from the anterior part of the postcaval, between the liver and pericardium, but I have never succeeded in getting any injecting fluid* to pass along the whole length even of the larger vessels. Many of the arteries can be injected with greater or less success from the conus arteriosus and cœliaco-mesenteric artery, but the delicacy of their walls makes this a difficult process. Although I have thus obtained injections of most of the branchial vessels and larger veins, the pulmonary arteries, and the proximal ends of most of the chief branches of the aorta, the ultimate distribution of many of the latter could not be further elucidated by these means. I was also unable to make satisfactory injections of the hepatic-portal and renal-portal veins. But even without injection, many interesting details can be made out, and entire sections of the animal have aided much in supplementing and checking my dissections.

Arteries.

Four afferent branchial arteries arise on either side, close to the conus arteriosus, arranged in an anterior and a posterior pair (Pl. XIV., fig. 44), so that one can hardly speak of a ventral aorta. These curve forwards and outwards, and pass respectively to the 1st, 2nd, 3rd, and 4th branchial arches (*af. br.* 2–5). From Boas's description (5) it appears that the anterior pair carry blood which has been purified in the lungs, while the posterior pair contain almost unmixed venous blood from the right atrium.

* For injection I made use of various substances, viz., Teichmann's "Injectionsmasse," plaster of Paris, gelatine, and Berlin-blue in water.

The afferent artery of the first branchial arch (*af. br.* 2) gives off a vessel just ventrally to the hyobranchial cleft, which is continued forwards to supply the submaxillary region (*s. mx.*), and which close to its origin gives rise to a hyoidean artery (*af. br.* 1) which passes upwards and outwards along the inner face of the hyoid arch to supply the "opercular gill"; this gill, therefore, apparently receives arterial blood.

The arteries of the first and second branchial arches (*af. br.* 2 and 3) pass directly up the latter, which bear no gill lamellæ, and the afferent thus pass directly into the efferent trunks dorsally (*ef. br.* 2 and 3). The remaining two trunks, corresponding to the third and fourth branchial arches respectively (*af. br.* 4 and 5) carry venous blood, supplying the complete gills borne on each of these arches. From the dorsal end of the fourth, a vessel arises which curves round so as to pass to the hemibranch on the anterior face of the fifth branchial arch (*af. br.* 6). This fact supports Boas's view as to the origin of the lamellae on the fifth arch stated above. From the arteries of the second, third, and fourth branchial arches a small branch is given off dorsally to the first, second, and third external gills respectively (*af. e. br.*).

It appears from Bischoff's and Hyrtl's descriptions that in Lepidosiren there are only three main afferent arteries, the fourth being absent, and that both the fourth and fifth branchial arches are supplied by a small dorsal branch from the third efferent branchial. Four complete arches are present in Ceratodus, but Günther does not describe the blood supply of the hemibranch of the fifth arch.

Even in Ceratodus, all the efferent branchial arteries unite into a large common trunk on either side before joining the dorsal aorta, and in Protopterus and Lepidosiren, owing to the greater reduction of the branchial apparatus, and its consequent compression into a relatively smaller area, the fusion of the efferent vessels is still more marked, the common transverse trunk to which they give rise (*rt. ao.*) being relatively longer. This trunk is made up of four main factors:—1st, the common trunk formed by the union of the efferent vessels from the hyoid and first branchial arch; 2nd, the efferent vessel of the second branchial arch; 3rd, that of the third arch; and 4th, that of the fourth and fifth arches.

The first of these gives off, near its origin, a small vessel (*plt.*) which runs forwards in the mucous membrane of the roof of the mouth, as far as the nasal region. This may be called the palatine artery. A short distance externally to it, the main trunk bifurcates over the hyobranchial cleft, the anterior or hyoidean branch giving off a carotid (*car.*) after emerging from the hyoidean hemibranch (*cf. br.* 1). This carotid apparently supplies the external parts of the head, and enters a fossa in the skull beneath the trigeminal nerve.* The posterior branch can be traced down the first branchial arch (*cf. br.* 2) becoming continuous with the corresponding efferent artery.

The second efferent branchial artery (*cf. br.* 3), which is the largest of all, has a corresponding course and arrangement to the first, and is similarly connected with its afferent artery. These two thus resemble the aortic arches of the Holocephali and Teleostei in possessing a single efferent artery to each gill arch. The third and fourth efferent branchials of Protopterus (*cf. br.* 4 and 5) on the other hand, resemble the revehent trunks of Elasmobranchs in the fact that each is made up of two vessels which run externally to the corresponding afferent artery, between it and the cartilaginous arch, and join with one another dorsally to the gills. The trunks thus formed unite with one another and with the second afferent branchial, and enter the aortic root before the latter is joined by the first efferent branchial, the second and third first uniting, and the fourth joining them immediately afterwards. The efferent vessel of the fifth arch (*cf. br.* 6) is single, as there is only a hemibranch in this position: it joins the fourth close to the junction of the two factors of the latter.

* My observations with regard to the vessels which supply the head are so incomplete that I have purposely left out any reference to their morphology. The vessel I have called the palatine artery may correspond to Peters's "posterior carotid" and to Boas's "internal carotid," and that which I describe simply as carotid may represent Peters's "anterior carotid." The account Günther gives of the carotid in Ceratodus refers only to its proximal portion, and it apparently represents the common base of the efferent hyoidean artery.

For recent contributions to this subject in Elasmobranchs, *cf.* T. J. Parker, "On the blood-vessels of *Mustelus antarcticus*," Phil. Trans. vol. clxxvii., pt. II., 1886; and H. Ayers, "The Morphology of the Carotids," Bulletin of the Museum of Comp. Zool. at Harvard Coll., vol. xvii., No. 5, 1889.

The efferent vessels of the external gills (*cf. e. br.*) are situated dorsally to the corresponding arteries (*cf.* Pl. x., fig. 20), and enter the efferent trunks of the second, third, and fourth branchial arches. Their small size renders an accurate dissection of them very difficult, and it is more easy to make out the details of their relations by means of serial sections. Peters does not figure or describe the vessel from the small third external gill: so far as I could make out it enters the main trunk near the origin of the pulmonary artery.

Peters describes and figures only *one* pulmonary artery, viz. that of the left side. But Hyrtl has shown that in Lepidosiren this vessel is paired, and has apparently quite similar relations to that of Protopterus, which was described in my preliminary paper (21).*

It arises on either side from the aortic root just internal to the junction of all the efferent branchial vessels (*p. a.*). The left (*p. a.*[1]), or ventral pulmonary artery,† is rather the larger of the two, and is the one described by Peters. It passes backwards, inwards, and slightly downwards, so as to reach the ventral surface of the lung, along which, after crossing the left pulmonary vein, it extends as a median vessel for about one-third of the length of the lung, and then forks (fig. 46). The exact point of bifurcation appears to vary somewhat in different individuals, but it is always some distance behind the junction of the median and paired portion of the lungs. Thus for some distance the single artery lies on the ventral side of the closely applied walls of the two lungs. After the bifurcation, each branch passes backwards along the ventral and inner margin of the lung to its posterior end (figs. 44 and 46, and Pl. x., fig. 21).

* In the recent Paper by Röse, already referred to, the author was apparently not aware that the right pulmonary artery of Protopterus had already been described, and he makes no mention of Hyrtl with regard to this vessel in Lepidosiren. He states that the pulmonary vessels arise from the fourth efferent branchial, and speaks of the postcaval as the "hepatic vein" ("Lebervene.")

† Boas states that this artery gives off anteriorly a branch to the œsophagus, and his statement is supported by Röse: although in one specimen I thought a small branch could be seen where the artery crosses the œsophagus, I cannot be certain on this point. In Lepidosiren, according to Hyrtl, the inferior pulmonary artery gives off intercostal arteries posteriorly: this seems improbable.

The right or dorsal pulmonary artery (figs. 44 and 47 *p. a.*[2]) passes, dorsally to the cœliaco-mesenteric, on to the dorsal surface of the lungs, and bifurcates close to the anterior end of the latter, just behind the crossing of the pulmonary branches of the vagus. Each vessel then extends backwards along the lung on the inner side of the corresponding nerve (*cf.* fig. 21).

Boas (5) has shown that the arrangement of the pulmonary arteries in Ceratodus is essentially similar to that described above for Protopterus. The left is the larger of the two: both extend for some distance dorsally to the œsophagus, right and left of the aorta; the left then passes ventrally to the œsophagus, so as to extend along the ventral surface of the lung.*

This remarkable arrangement of the right and left pulmonary artery becoming respectively dorsal and ventral in position is therefore common to all the Dipnoi. Like the crossing of the pulmonary branch of the vagus, it is possibly to be explained by a twisting of the lungs during development, as already mentioned.

It appears from the researches of Boas,† to be a general law amongst air-breathing Vertebrates that the pulmonary artery is developed in connection with the sixth primary aortic arch of the embryo, that is, from the fourth branchial arch. This is apparently easy to recognize in Ceratodus, but in Protopterus the pulmonary arteries do not arise directly from the fourth efferent branchial arteries, but from the aortic roots. This is probably to be explained by the reduction of the branchial apparatus, which has modified the primary positions of the vessels.

The cœliaco-mesenteric artery (Fig. 44, *c. m. a.*) arises from the aorta a short distance from its anterior end, and about one-sixteenth of an inch behind the junction of the skull and notochord. It extends backwards and outwards towards the right side, hidden in the oblique cleft between the lobes of the liver, and gives off two anterior hepatic arteries (*hp. a.*) just

* The arteries supplying the air-bladder in Amia (Ramsay Wright, "Riverside Nat. Hist.," Standard Nat. Hist., New York, p. 48, vol, iii., fig. 43), and Polypterus (Johannes Müller, "Ueb. d. Bau u. Grenzen d. Ganoiden," Berlin, 1846, p. 33, Taf. iii, fig. 2) apparently have a similar origin to the pulmonary arteries of Ceratodus, with which they are very probably homologous.

† "Ueber die Arterienbogen der Wirbelthiere."—Morphol. Jahrbuch, Bd. XIII., 1887.

before entering the cleft. On emerging from the latter it curves round the posterior side of the gall-bladder, and gives off gastric, cystic, and pancreatic branches (fig. 44; Pl. XI., figs. 28 and 29, and Pl. XII., fig. 31 *c. m. a.*, *g. a.*, *cy. a.*, *pan. a.*) The main trunk (*m. a.*^{1}) then passes to the wall of the bursa entiana, and gives off a posterior hepatic branch (*hp. a.*^{1}) just before entering the latter close to the pylorus, and side by side with the bile-duct and portal vein. From this point it extends down the axis of the spiral valve as the intra-intestinal artery (Pl. X., fig. 21, and Pl. XII., figs. 32 and 33, *m. a.*^{1}), much as in Mustelus and Scymmus.* Sections appear to show that there is also a ventral intestinal branch (fig. 33, *m. a.*$^{v.}$), as in these fishes, and smaller branches also supply the walls of the intestine, but the connections of these I have not succeeded in following out (*cf.* 7 and 12).

The paired subclavian artery† (fig. 44, *s. cl. a.*) arises from the aorta close behind the cœliaco-mesenteric, and passes to the pectoral fin ventrally to the muscles of the cranial rib, which receive on either side a special branch from the aorta (*cr. a.*).

Numerous intercostal arteries (*cf.* 34) arise from the aorta along its whole length, there being usually one to each muscular segment, though they have not a perfectly regular arrangement, and do not always arise quite opposite to one another.

The anterior mesenteric artery (*m. a.*^{2}) arises far back, a short distance in front of the pelvic arteries (*pl. a.*). It extends downwards and forwards in the mesentery, and reaches the intestine close to the last turn or last turn but one of the spiral valve. Thence it passes forwards in the intestinal wall as the dorsal intestinal artery (figs. 21, 28, and 33, *m. a.*^{2}), and, apparently (but of this I am not certain), sends off a posterior branch to the part of the intestine behind this point. Branches from this vessel can be seen in the intestinal walls, and its relations are apparently similar to

* *Cf.* T. J. Parker (*loc. cit.*).

† In Ceratodus, according to Günther, there is a branch of the cœliac "destined for the dorsal surface of the lung" and another to the kidney, and the left subclavian sends off two small vessels to the testis, while another branch forms a very peculiar anastomosis with the left "vena cava superior," a similar anastomosis being also indicated on the right side. These points certainly require further investigation.

those of the anterior spermatico-mesenteric, or anterior mesenteric, of Elasmobranchs.

About one-eighth to one-fourth of an inch behind the anterior mesenteric another small vessel arises from the aorta, and passes downwards and forwards parallel to the former (*m. a.*[3]). The exact course and distribution of this vessel I have not been able to determine, but I believe that it passes backwards to the walls of the cloaca, and also supplies the cloacal cæcum. It may probably be described as the posterior mesenteric artery (*cf.* 12).*

The pelvic arteries (*pl. a.*) correspond to a pair of intercostals which are rather larger than the others; they pass downwards and backwards in the body-wall, parallel to the ribs, to enter the pelvic fins. They do not correspond to the *last* pair of intercostals, as several pairs of ribs are present behind their origin.

The kidneys are supplied by several vessels (*r. a.*) most of which arise directly from the aorta, posteriorly as well as anteriorly to the pelvic arteries. A left renal artery is also given off from the anterior mesenteric, and a right from the posterior mesenteric.

Numerous small branches from the aorta supply the gonads and oviducts, but the exact number of these and their relations to the renal vessels I have not been able to make out.

The aorta is continued into the tail, entering the hæmal canal, and having the usual position between the notochord and caudal vein (Pl. x., fig. 22, *c. ao.*).

Veins.

A short precaval vein (*ductus Cuvierii*) penetrates the pericardium and opens into the right division of the atrium on either side (Pl. XIV., fig. 45, *pr. c.*). An inferior jugular (*i. j.*), from the floor of the mouth, enters it anteriorly, and just posterior to this a short trunk opens into the precaval: this is formed by the junction of the jugular (anterior cardinal, *j.*) and

* This name would probably apply according to Howes's definition of the vessel in question (*loc. cit.*), though such an interpretation militates against the supposition of the homology of the cloacal cæcum with the appendix digitiformis of Elasmobranchs.

subclavian (*s. cl. v.*) veins. I have not followed out any further details with regard to the factors of these veins.*

Two large veins (fig. 45, Pl. x., fig. 21, and Pl. xv., figs. 49, 51, and 53, *pt. c.*, *cd. v.*), which have been described as a paired "vena cava posterior" by previous observers, take their origin from the revehent renal veins, and pass along the body to enter the sinus venosus. Except that the right is considerably larger than the left, these two vessels have a close similarity as regards their posterior section, each running along the ventral side of the kidney, partly imbedded within the lymphoid and fatty investment of the latter. But anteriorly to the kidney an important difference is seen in the course of the two veins. The left (*cd. v.*) surrounded by lymphatic tissue, passes along the dorsal border of the corresponding gonad, just ventrally to the lung, and then continuing its course, opens into the left precaval. The larger right vessel (*pt. c.*) on leaving the kidney anteriorly, passes forwards, imbedded in the dorsal border of the liver, from which it receives the hepatic veins (*h. v.*). In front of the liver it emerges, supported by a special mesenteric fold, and instead of joining the corresponding precaval, turns medianwards, so as to penetrate the pericardium in the middle line on its dorsal and posterior side. It then opens into the sinus venosus.

In my preliminary account of Protopterus (21) I expressed the opinion that these veins correspond to more or less modified posterior cardinals, and not to a paired postcaval. But at that time I had only made a superficial examination of the course of these vessels, and in a subsequent Paper (22) gave what I believe to be the true interpretation of their homology, viz. that the left vein represents the left posterior cardinal, and the right the postcaval of higher Vertebrates.

This determination is supported by Hochstetter's views as to the origin of the postcaval.† He has shown that in Amphibia the posterior part of

* Hyrtl's account of them in Lepidosiren is somewhat peculiar. Besides other factors, he states that the jugulars receive branchial veins from the third to the fifth arches.

† "Beiträge zur vergl. Anat. und Entwickelungsgeschichte des Venensystems der Amphibien u. Fische," Morphol. Jahrb. Bd. 13, 1887–8. Hochstetter has given additional support to his views by researches on the Amniota ("Ueb. die Bildung d. hinteren Hohlvene bei Säugethieren," Anat. Anz., II. Jahrg, 1887; "Beiträge zur Entwickelungsgeschichte des Venensystems der

the vena cava is formed by the fusion of that portion of the cardinals which receive the revehent renal veins, and which he speaks of as the "Urnierenabschnitt." The anterior part of the cardinals, lying in front of the kidney, either persists as the azygos vein (as in the Salamander) or else disappears entirely (as in the Frog).*

A single caudal vein † (*c. v.*, see also fig. 21,) runs beneath the caudal aorta, enclosed within the hæmal canal. On emerging from the latter, it soon bifurcates to form a paired renal-portal (*r. p.*) each of which passes along the dorsal and outer side of the kidney, surrounded by lymphoid tissue, and gives off advehent renal veins along its course which form a network on the dorsal surface of the kidney (Pl. xv., fig. 51). A number of veins, having a more or less regular segmental arrangement, emerge from the body-walls laterally all along the cœlome, and then extend inwards along the peritoneal folds which support the various viscera (*pa. v.*). The posterior of these, in the region of the kidneys, enter the renal portals, while the anterior open into the postcaval (through the liver) and cardinal respectively. Vertebral veins (*v. v.*), appearing in the cœlome close alongside the notochord, apparently open into the same vessels as the parietal veins. The number of these I cannot state definitely. A pelvic vein (*pl. v.*) opens into each renal portal near the posterior end of the kidney.

The veins from the generative organs as well as from the kidneys form a network just beneath the peritoneum, covering the ventral surface of the gonads (figs. 49 and 53), and they open into the postcaval and cardinal respectively ‡ at intervals along the whole length of the gonads.

Amnioten," Morph. Jahrb., Bd. 13, 1887–8; and "Ueb. das Gekröse d. hinteren Hohlvene," Anat. Anz., III. Jahrg, 1888).

* This view is further supported by the occasional persistence of one or both azygos veins, or of one entire posterior cardinal amongst Anura (*cf.* Howes "On the azygos vein in the anurous Amphibia," Proc. Zool. Soc., 1888, and 22).

† Hyrtl describes a *paired* caudal vein in Lepidosiren, but this condition probably only refers to the continuation of the vein anteriorly to the hæmal canal, *i. e.* to the posterior part of the renal portals. The paired caudal is said to receive numerous small veins from the "bladder," as well as two from the body-walls. Bischoff also describes the renal portals.

‡ By an oversight it was stated in (22) that the genital veins opened into the renal portal. Hyrtl states that the smaller ones are connected with the right vena cava (= right cardinal) and the larger ones with the renal portal in Lepidosiren.

In their renal section, the postcaval (which here represents the unmodified posterior portion of the right cardinal) and left cardinal are connected by transverse anastomoses (*ans.*) which are usually three, and sometimes four, in number. At their junction with the latter they are usually much branched, and form networks.

The hepatic veins (*h. v.*) are numerous, and open into the postcaval all along its course through the liver; the anterior one (or two) which joins the postcaval just before the latter leaves the liver, is considerably larger than the others.

One or two small œsophageal veins (*æs. v.*) enter the cardinal a short distance behind the heart.

I have been able to find no trace of a right azygos, representing the anterior section of the right cardinal: apparently this disappears entirely. But, although the main veins of Lepidosiren are quite similar to those of Protopterus, Hyrtl describes a paired azygos running alongside the aorta in addition to the "venæ cavæ posteriores." But it seems unlikely that this vessel is correctly named and described, for Hyrtl's left "vena cava posterior" has precisely the relations of a cardinal, and if the azygos is present at all, it is probably an independently formed vessel.

The veins of Ceratodus also need a further examination, which would, I think, confirm the view I have stated elsewhere (22). Günther's description of them (7) is not complete enough to warrant any definite conclusions being drawn. But if, as I have ventured to suggest, Günther is mistaken in his description of the caudal vein, and the median and two lateral veins figured on Pl. XLI., fig. 3, of his memoir, represent the caudal and pelvic veins, it is easy to compare all the main veins of the body in Ceratodus with those of Protopterus: the chief difference would then be that the anterior part of the left cardinal has apparently disappeared, and that Günther's left "vena cava posterior" represents its persistent renal portion, which instead of passing into the left precaval as in Protopterus, empties all its blood into the postcaval by means of the transverse anastomoses. If this is the case, Ceratodus shows an advance on Protopterus as regards the importance of the postcaval and the consequent reduction of the cardinal system, and more nearly approaches the condition seen in the Amphibia,

in which *both* cardinals take part in the formation of the postcaval. But this one would not expect, as Ceratodus is less specialized towards a terrestrial type than are the other two genera.

The main factor of the hepatic portal vein (fig. 45, and Pl. XI., figs. 28 and 29; Pl. XII., fig. 31, *h. p. v.*) is a large mesenteric vessel, which runs close to the intra-intestinal artery in the axis of the spiral valve, and comes to the surface at the pylorus (Pl. X., 21, and Pl. XII., figs. 32 and 33, *i. int. v.*). There is also apparently a ventral intestinal vein,* the details of which I have not made out. Just anterior to the pylorus, the mesenteric vein can be traced into an anterior and posterior branch, the latter supplying the posterior lobe of the liver, behind the gall-bladder, and the former receiving a large lieno-gastric vein (the factors of which form a dense meshwork in the spleen) and a pancreatic vein, and then dividing into branches which supply the anterior lobe of the liver.

Each pulmonary vein (fig. 46, *p. v.*) runs along the outer border of the corresponding lung, and at about the anterior third of the latter, gradually turns medianwards, and unites with its fellow on the ventral side of the unpaired portion of the lung, considerably anterior to the bifurcation of the ventral pulmonary artery. The unpaired pulmonary vein thus formed curves round to the right side of the vestibule, and penetrates the pericardium to enter the small left atrium, being closely connected with the sinus venosus, so as to appear sunk into the latter.

I have nothing definite to record with regard to a lymphatic system, and doubt whether lymph-vessels with independent walls are present.†

* *Cf.* T. J. Parker (*loc. cit.*).

† *Cf.* Hochstetter (*loc. cit.*); Ayers (1) and Paul Meyer, "Ueb. Eigenthümlichkeiten in den Kreislaufsorganen der Selachier."—Mittheil. aus der zool. Station zu Neapel, Bd. VIII., 1888.

Urinogenital Organs.

General Part.

The most recent and complete account of the general relations of the urinogenital organs is that of Ayers (1). The kidneys are elongated bodies lying close to the ventral side of the lungs, and extending along about the posterior two-thirds of the body-cavity. They are closely invested by a mass of lymphoid and fatty tissue, which, posteriorly, forms a rounded plug fitting into the hinder end of the cœlome, and closely binding the two kidneys together in this region (Pl. VII., fig. 1; Pl. x., fig. 21; Pl. XV., figs. 49, 51, and 53; and Pl. XVI., figs. 56–61). Anterior to this junction, irregular masses of lymphoid tissue also occur between the kidneys (figs. 49 and 53). From about its middle, each kidney gradually tapers off towards the anterior end, the one of the right side coming into close contact with the liver at the point where the postcaval enters the latter organ (Pl. XIV., fig. 45).

Laterally, the lymphoid and fatty investment of each kidney is closely applied to a similar mass of tissue surrounding the corresponding gonad, on the lower side of which it projects as a tapering ridge, giving the whole organ—gonad and investing tissue—a pear-shaped form in transverse section (Pl. x., fig. 21, and Pl. XVI., figs 57 and 59). On their outer side, the renal and generative organs are in close apposition to the body-walls, and they together form an arched roof over the intestine (fig. 21), extending down on either side of the latter so as even to meet one another ventrally in ripe specimens. The gonads are supported by peritoneal folds which arise from the body-walls laterally, and in which the blood-vessels from the latter run. The peritoneal covering is especially thick on the inner side of the gonad which looks towards the intestine, and this is continuous dorsally with that covering the inner (ventral) surface of the kidney, round the dorsal side of which organ the peritoneum extends, beneath the lung, but is absent more laterally, where the kidney is in contact with the body-

walls. The exact relations of the peritoneum are, however, by no means easy to follow, as it does not consist of simple folds, but gives rise to a delicate meshwork of connective tissue filling up a good part of the space between the body-walls and the viscera, as in Lepidosiren (12) and Ceratodus (7).

In unripe specimens the gonads have a similar form in both sexes, and each appears like an elongated smooth band, the posterior half or two-thirds of which is of about the same diameter throughout, while more anteriorly the organ gradually tapers off, and its outer (ventral) border may be slightly lobed. The right gonad is usually, but not always, rather shorter than the left* (figs. 49 and 53), and lies close above the liver, to which it is united by connective tissue.

The lymphoid and adipose tissue investing the urinogenital organs has already been referred to. It more or less completely surrounds the gonads and kidneys, but is more especially aggregated along the borders of these organs, as well as between the kidneys. That along the outer border of the kidney is penetrated by the renal portal vein (Pl. xv., fig. 51, *r. p.*), while on the inner border, the cardinal (or postcaval) vein (figs. 49, 53, and 56) is partially imbedded in this tissue, a dense mass of which lies between the kidney and the corresponding gonad, and to a greater or less extent hides the Müllerian duct from view (figs. 21, 51, and 53). In structure, this tissue resembles the large-celled lymphoid tissue in connection with the alimentary canal, but no compact masses of smaller cells ("follicles") are present in it, and in many places it passes insensibly into adipose tissue, to which it undoubtedly gives rise. The adipose tissue is more or less completely surrounded by lymphoid cells, and is most abundant in the thicker portions of the lymphoid investments, both of the kidneys and gonads (figs. 56–61). But no sharp line of demarcation can be drawn between these two kinds of tissue, lymphoid cells being present irregularly amongst the fat-cells.

We find here, therefore, an arrangement somewhat similar to that seen amongst Teleosts and Ganoids—in which the renal tissue is closely

* Ayers states (1) that the two were equal in length in the specimens he examined, and in one male I found the left testis to be the longer of the two.

surrounded, and even partially replaced, by lymphoid tissue*—and in the Amphibia, in which the large "corpora adiposa" are lymphoid structures which give rise to fat-cells.†

Around the kidney, but more particularly along its dorsal and outer sides, masses of brown cells are present, which in appearance remind one of the adrenal bodies of Amphibia (fig. 56, *p. g.*[1]). These have a similar structure to the yellow and brown pigment cells met with along the alimentary tract (p. 83). Whether they, or the lymphoid cells which give rise to them, have anything to do with the adrenals, I am unable to say: the presence of adrenals is not known in Lepidosiren (12) or Ceratodus (7).

Renal Organs.

Each kidney is somewhat oval in transverse section (Pl. XVI., fig. 56), and gradually tapers off towards its anterior end (Pl. XV., figs. 49, 51, and 53). In Ceratodus (7) the kidneys are lobulated, and this is also said to be the case by Ayers (1) in older individuals of Protopterus. But according to my observations, they are always compact, and show no trace of a division into lobes, and thus resemble those of Lepidosiren (12). In order to see their form, it is necessary to dissect away the investing tissue.

The renal duct (*k. d.*) lies imbedded in the ventro-lateral border of the kidney, towards the posterior end of which it becomes more superficial, so as to be easily recognizable when the investing tissue is removed; for this

* *Cf.* Balfour, "On the nature of the organ in adult Teleosteans and Ganoids, which is usually regarded as the head-kidney or pronephros," Quart. Jour. of Micros. Science, vol. xxii., N.S., 1882; W. N. Parker "On the Kidneys of Teleostei," Brit. Assoc. Reports, 1882; and S. Grosglik, "Zur Morphologie der Kopfniere der Fische," Zool. Anz., Jahrgang VIII., 1885, p. 605, and IX., 1886, p. 196. Ayers states that a gradation exists between the lymphoid organs of Teleostei, lymphoid and adipose bodies of Amphibia, and the exclusively adipose structures in Reptilia.

† Whether this investing tissue in Protopterus corresponds to modified portions of the primitive renal and reproductive organs of the embryo, it is naturally impossible to state without a study of their development. That such a modification or degeneration may occur in connection both with the kidneys and gonads is now well known in many cases (*cf.* note above, and Rosenberg, "Untersuch üb. die Entwick. der Teleostierniere," Dorpat, 1867; Weldon "On the head-kidney of Bdellostoma, with a suggestion as to the origin of the supra-renal bodies," Quart.

covers it even after it becomes free from the kidney. The free portion is very short, and turns medianwards, so as to be enclosed with its fellow in a common sheath just before entering the dorsal wall of the cloaca. But each duct opens independently into the cloaca just posterior to the genital papilla* (fig. 53, *k. d.*[1], *g. p.*), being enclosed, along with the latter, in a common urinogenital sinus in the male (figs. 49 and 50, *u. g. s.*, *g. p.*, *k. d.*[1]). It will thus be seen that the urinary and generative ducts open quite independently of the cloacal cæcum (*cf.* fig. 54), whereas in Ceratodus they are said by Günther to open into the latter.

The kidney is made up of numerous coiled urinary tubules, provided with glomeruli, and, on the whole, converging towards the ventral side (fig. 56). Towards the posterior end, a number of large collecting tubes can be seen entering the duct. Each tubule is composed of a single layer of columnar cells, enclosing a central lumen. The capillary network is extremely dense, and separates the tubules from one another by considerable intervals. The ducts are also lined by a single layer of columnar epithelium.

The presence of nephostomes in adult Elasmobranchs and Amphibians† would not unnaturally lead one to expect that they would be found in the Dipnoi. Ayers (1) states that they are absent in Ceratodus, but he believed them to be present in Protopterus, although he was unable to prove their existence by means of sections. He says (p. 486)—"Auf der Ventralseite der Nieren des Lepidosiren (= Protopterus) sieht man auf dieser Peritoneal-

Jour. Micros. Science. vol. xxiv., N.S., 1884; Giles, "Development of the fat-bodies in *Rana temporaria;* a contribution to the history of the pronephros," Studies from the Biol. Lab. of the Owens College, Manchester, p. 123, vol. ii., 1890; Milnes-Marshall and Bles, "Development of kidneys and fat bodies in the Frog," p. 133 of the same Journal). In the last-mentioned Paper the authors correct Giles's view that the pronephros becomes converted into the fat-body, which they state is developed from the anterior end of the genital ridge.

* Owen (20) and M'Donnell (18) wrongly state that the ureters open into the common termination of the oviducts in the female.

† *Cf.* Balfour, "Development of Elasmobranch Fishes," 1878; C. Semper, "Das Urogenitalsystem d. Plagiostomen u. seine Bedeutung f. d. übrigen Wirbelthiere," Arbeit a. d. Zool., Zool. Inst. zu Würzburg, Bd. II., 1875; Spengel, "Das Urogenitalsystem der Amphibien," Arb. a. d. Zool., Zool. Inst. d. Univ. Würzburg, Bd. III., 1876.

decke unter geringer Vergrösserung ovale oder runde Vertiefungen oder Löcher, die augenscheinlich bis in die Organsubstanz reichen (fig. 53). Diese Oeffnuungen ("Nephrostomen") ähneln denen, die man bei den Nieren mancher Amphibien findet." What these apertures could have been I cannot form any idea, but I can state with certainty that no nephrostomes are present. And, moreover, their existence as functional structures in Protopterus is rendered practically impossible on account of the kidneys being surrounded by so dense a mass of investing tissue, which would effectually cut off their communication with the cœlome.

Generative Organs of the Male.

Up to the present time there has been no satisfactory description of the male generative organs of Protopterus, even as regards their macroscopic characters, and I am inclined to think that in cases where an account of them has been given (14, 24, and Wiedersheim's Lehrbuch, 1st Ed.) it has referred to the organs of an unripe female, which superficially closely resemble those of the male.* In both sexes the organs are so closely walled in by tissue resembling that covering the kidneys, that in young or badly-preserved specimens it would be almost impossible to tell one from the other, except in the case of females with ripe eggs.

The general form and relations of the testis have already been described (figs. 49 and 51). In fig. 49 the peritoneum covering the ventral (internal) face of the testis and gonad has been left entire on the left side (right in figure) and the testicular veins (*ts. v.*) can be seen entering the cardinal (*cd. v.*). On the right side (left in figure) the peritoneum as well as the underlying lymphoid tissue have been removed on the ventral surface: such a dissection at once reveals the difference in structure between the testis and the ovary. The testis (*ts. l.*) then appears as a closely-coiled and lobulated mass, which is broad in about the posterior two-thirds of the organs, and gradually thins out anteriorly. The relations of the investing tissue can

* M'Donnell (18) figures the testes (?) but gives no account of them and their ducts, and he seems to have mistaken a male for a female in describing the terminations of the urinogenital ducts.

be seen in figs. 49 and 51 (*ly. ad.*) as well as in the sections represented in figs. 57–61. On the dorsal (external) side of the gonad the peritoneum is much thinner than on the ventral (internal) surface, and the testis can thus be seen through it (see fig. 51).

From the statements of previous observers, it has usually been supposed that in the Dipnoi the products of the testis pass to the exterior through a duct which is the homologue of the oviduct of the female. Thus Peters (24) states that "die Hoden der Männchen haben einen gewundenen Ausführungsgang am äusseren hinteren Rande der Hoden," and Klein (14) also mentions the presence of "ein feiner gewundener, wohl Ausführungsgang." Ayers (1) thought it not improbable that this so-called "vas deferens"—which, he says, doubtless corresponds to the Müllerian duct—has no function in male Dipnoans, and that the sperm passes to the exterior through the abdominal pore.

In Ceratodus (7), Günther states that "the *vasa deferentia* are, with regard to their course and orifices, entirely analogous to the oviducts. They are "attached to the ventral margins of the ureters," have "a slightly undulated course," open anteriorly into the body-cavity, and "terminate in a common opening in the dorsal wall of the cloaca" (*i. e.* the dorsal diverticulum of the cloaca): this opening "is separated from that of the ureters by a low fold of mucous membrane." "In their anterior third they are very thin, but their lumen is nearly 2 millims. wide. They gradually become narrower, until, in the middle of their length, the diameter of the duct is scarcely more than half a millim. Posteriorly they widen again, and the wall becomes thicker, the mucous membrane being raised into longitudinal folds; but even towards the end they are scarcely half as wide as the ureter." In his description of the testis, Günther states that "a duct traverses the whitish substance from one end of the testicle to the other (Pl. 40, figs. 3 and 4*a*.); it is widest in the middle (scarcely one-sixteenth of an inch) and tapers towards its extremities, without penetrating to the surface of the testicle; its walls are perforated by innumerable pore-like openings, leading immediately into the *canalicula seminiferi* (*d*)." The course of these canaliculi is described; and it is stated that they can be injected from the longitudinal duct, and

that they "run parallel to one another, across the testicle, at a right angle to its longitudinal axis; they have a slightly wavy course, do not subdivide, and appear to be equally wide throughout their length." "There is no connection between the ureters and the testicles," and "no direct communication between the testicle and *vas deferens*."

In a male specimen of Protopterus in which the testis contained no ripe spermatozoa, I have been able to trace a fine duct, passing between the gonad and kidney on either side, which has precisely the relations of the oviduct in the female (fig. 51 and 60 *m. d.*). At the anterior end of the testis, it enlarges slightly, and opens into the body-cavity by a funnel-shaped aperture, with folded walls (figs. 51 and 61 *m. d.*[1]). The rest of the duct is of a very small diameter, and becomes especially fine in the middle part of its course, in which I have been unable to distinguish a lumen. Anteriorly (see fig. 60) as well as posteriorly (fig. 52) a lumen can be traced for some distance, surrounded by a layer of columnar epithelium. In other individuals, in which the spermatozoa were ripe (even though not much larger than the specimen above described) I was unable to recognize this duct at all, and it seems probable, therefore, that it becomes aborted in the adult.

At the posterior end of the testis, this duct is connected with a larger one, which leaves the testis at its postero-internal border (fig. 51, *sp. d.*). Transverse sections through this region clearly show the uniting of these two ducts into a single one (fig. 52). The latter lies externally to the kidney duct, and gradually bends inwards so as to unite with its fellow before entering the dorsal wall of the cloaca. In this manner a genital papilla is formed, as in the female, and this is enclosed, along with the apertures of the kidney duct, in a common urinogenital sinus (figs. 49 and 50, *u. g. s.*). The latter is conical in form, and opens into the cloaca by an aperture situated towards the ventral side of its apex. There is no direct communication between the testis and the tubules of the kidney. The duct which emerges from the testis I will speak of as the sperm-duct. Its free portion is all that can be seen externally.

Transverse and longitudinal sections through its middle or posterior broader portion, show the testis to be made up of several coiled lobes

(figs. 57 and 58), while in the anterior narrower part it consists of a single lobe (fig. 59), the whole being surrounded by the investing tissue. Each lobe is composed of a number of coiled seminal tubules. In the anterior part a slight depression can be seen along the median ventral line of the single coiled lobe, and in this the sperm-duct lies imbedded (fig. 59, *sp. d.*). In the posterior part, the duct is situated in a depression between two contiguous lobes (fig. 57), and longitudinal sections show that it follows the coils of the lobes (fig. 58). The duct is lined by a single layer of columnar epithelial cells, and into it the seminal tubules open (figs. 58 and 59). If a section is taken so as to cut the tubules of any lobe longitudinally, it will be seen that they radiate outwards from the duct (fig. 59). Each seminal tubule is composed of a number of rows of seminal cells, enclosing a central lumen, which in ripe specimens is seen to be filled with spermatozoa (figs. 57–59).*

The spermatozoa (fig. 62) are remarkable for their minute size, as well as for the presence of *two* flagella, representing the so-called "tail." The "head" is carrot-shaped, and nearly resembles that of the spermatozoa of *Bufo cinereus*† and of *Salamandra maculosa*.‡ But in both these cases the "tail" is single, while in Protopterus it consists of two distinct and separate vibratile filaments, and thus has a form which is apparently unique amongst Vertebrates. These flagella are very delicate, and taper off gradually. As far as I could trace their fine ends, they seem to be rather shorter than the head, with which they are connected by a short neck ("Zwischenstück"). The head measures, in fresh specimens, about 40 μ in length, and about 10 μ at its greatest diameter. In the minute size of the spermatozoa, it will be seen that Protopterus differs greatly from Amphibians: in *Discoglossus pictus*, for example, the spermatozoa reach a length of over two millimetres (*vide* Spengel, *loc. cit.*). This is all the more remarkable, as most of the histological elements in Protopterus are exceptionally large.

* For a comparison with Salamandra, *cf.* F. Hermann, "Beiträge zur Histologie des Hodens," Arch. f. mik. Anat., Bd. xxxiv., 1889.

† Le Valette St. George, "Spermatologische Beiträge," Arch. f. mik. Anat., Bd. xxvii., 1886.

‡ Fleming, "Weitere Beobachtungen üb. die Entwick. d. Spermatozöen bei *Salamandra maculosa* maculosa,' Arch. f. mik. Anat., Bd. xxxi., 1888.

In many of the spermatozoa, a delicate oval investment, probably corresponding to the unchanged "cytoplasm" of the spermatic cell, is seen around the head, the pointed end of which protrudes beyond it, while it is attached at the base of the neck (fig. 62 c).

It is very possible that the double flagellum may represent a very primitive form of vertebrate spermatozoon. For in the case of various Vertebrates it is now well known that the tail of the spermatozoon is a complex structure, and that it consists of two primary parts—an axial portion, which may be further subdivided, and a spiral thread which winds around it.*

Generative Organs of the Female.

As regards the form and general relations of the female generative organs, I have little to add to the description of Ayers (1). In young individuals it is impossible, by a superficial examination, to distinguish between them and the corresponding organs of the male; but in ripe specimens (Pl. xv., fig. 53), the ova are seen projecting from the surface of the ovary (*ov.*), the outer (dorsal) side of which may be more or less lobed and irregular, and the oviducts (*ovd.*) can be indistinctly recognized through the peritoneum. The ova are less apparent on the inner than on the outer side of the ovary, on account of the thickness of the peritoneal coat, under which the ovarian and oviductal veins run to enter the postcaval or cardinal (*ov. v.*). The ripe ova are about 3·5 mm. in diameter.

The oviducts are imbedded in the lymphoid and adipose tissue between the ovaries and kidneys (Pl. x., fig. 21). In young specimens, each oviduct is a delicate tube, like its representative in the male, and is not coiled to any extent; while in ripe individuals its walls become very thick, and, except in the posterior third of its course, it becomes bent

* *Cf.* amongst others :—E. Ballowitz, "Das Retzius'sche Endstück der Säugethier-Spermatozoën," Internat. Monatschrift f. Anat. u. Physiol., Bd. VII., Heft 6; C. Benda, "Die neuesten Publicationen auf dem Gebiet der Samenlehre," Krit. Studie, Internat. Centralblatt f. d. Physiol. u. Pathol. d. Harn- u. Sexual-Organe, Bd. I., Heft 1; O. S. Jensen, "Untersuch. üb. d. Samenkörper d. Säugethiere, Vögel, u. Amphibien," Arch. f. mik. Anat., Bd. xxx., 1887; and Hermann (*loc. cit.*).

on itself in sigmoid coils, and closely resembles the oviduct of Amphibians. The ostia (*ovd.*[1]) are situated a short distance behind the pericardium: they are slit-like in form, and their walls are thin, and pass immediately into the thick glandular position. Posteriorly the two oviducts curve inwards towards one another, and unite before entering the cloaca (fig. 54, *ovd.*), on the dorsal wall of which they open by a single aperture situated towards the ventral side of the summit of a genital papilla, just anterior to the apertures of the renal ducts (*g.p.*, *k.d.*[1]).

The mucous membrane lining the oviducts, even in young specimens (fig. 21), is raised into a series of longitudinal folds, as in Urodeles. Of these there are about sixteen in the adult, and fewer in younger stages. In a transverse section of the oviduct (Pl. XV., fig. 55) these folds have the appearance of a series of simple glands, and in all probability they give rise to an albuminous envelope for the eggs.* Ayers states (1) that the oviducts swell considerably at the time the sexual products are ripe; and in fresh specimens highly refractive granules can be seen in the lining epithelium, and even in the lumen of the duct. It appears from Günther's description (7) that albumen is also secreted by the oviduct of Ceratodus.

The epithelium is made up of two rows of cells (Pl. XV., fig. 55; Pl. XII., fig. 35), the nuclei lying near the inner and outer borders respectively, and amongst them can be seen numerous smaller and more elongated nuclei, which stain differently from the others, and which I take to belong to migratory leucocytes (fig. 35, *leu.*). At the free edges of the folds the epithelium appears as if gnawed away in places, so that the underlying blood-vessels are seen close to the surface. Certain of the cells appear to be ciliated, while in others no cilia could be observed. I can hardly say how far these appearances may have been due to bad preservation; but they are certainly very similar to those Wiedersheim has recently described in the case of *Salamandra atra*, in which the epithelium not

* *Cf.* R. Stüve, "Beiträge z. Kenntniss des Baues der Eileiterdrüsen bei d. Amphibien."—Arch. f. mik. Anat., Bd. XXXIV.; Loos, "Die Eileiterdrüsen d. Amphibien u. Vögel."—Zeitschrift f. wiss. Zool., Bd. XXXV., 1881.

only degenerates, but the red and white corpuscles pass into the lumen of the oviduct, and are concerned in the nutrition of the young.*

The minute structure of the ovary has been described by Beddard (3); and although I am not able to support his statement as to the peculiar formation of certain of the ova by a fusion of the follicular cells, I have not made a sufficiently careful study of the ovary in different stages of development to warrant any discussion on the subject. It appears to me, however, that Ruge's† explanation of the appearances described by Beddard is certainly the correct one. He considers that they are to be explained as indicating a degeneration, and not as a development, of these ova, the follicular epithelium passing into the ovum, taking up the yolk-granules, and then disintegrating.

The Homologies of the Urinogenital Apparatus in the Dipnoi.

The determination of the homologies of the urinogenital ducts in the Dipnoi presents considerable difficulty, and this question can only be finally decided by a study of their development, and by a further examination of well-preserved specimens in all these species. At the same time I trust that the present paper will throw some light on the subject, and I will now venture to discuss the question briefly, making certain suggestions to which my work has led me.

In the female of Lepidosiren (12) and of Ceratodus (7), the urinogenital organs are apparently similar in most essential respects to those of Protopterus. In the male Lepidosiren, their structure is not known, and it appears from Günther's description of the male Ceratodus, that there is a considerable divergence between this animal and Protopterus. Apart from the lobulated form of the kidneys in both sexes, and from the fact that their ducts have a longer superficial course than in Protopterus, an important apparent difference is seen between the two genera with regard

* "Beiträge z. Entwick. von *Salamandra atra*."—Arch. f. mik. Anat., p. 469, Bd. xxxvi., 1890; *cf.* also Stüve, *loc. cit.*

† "Vorgänge am Eifollikel der Wirbelthiere."—Morph. Jahrb., p. 491, Bd. xv., 1889.

to the termination of the urinary and generative ducts, as already mentioned. In Protopterus, these open into the cloaca quite independently of the cloacal cæcum, while in Ceratodus their apertures are said to be situated on the apex of what appears to be the homologue of this structure.

Passing now to further details as regards the generative ducts in the male, we find that in both genera, at any rate in immature specimens, a duct similar to the oviduct of the female is present, extending between the testis and kidney; this opens anteriorly into the body-cavity, and posteriorly unites with its fellow so as to open into the cloaca by a common aperture. In Ceratodus, this aperture is separated from those of the renal ducts by a low fold of mucous membrane: in Protopterus it is situated on a genital papilla which is enclosed, along with the aperture of the kidney ducts, in a common urinogenital sinus.

In Protopterus, a sperm-duct, into which the testicular tubuli open, penetrates the substance of each testis, and on leaving the latter at its posterior end immediately unites with, and opens into, the representative of the oviduct above described. In Ceratodus, a duct having apparently a similar position and receiving a number of *canaliculi seminiferi*, is present, but this tapers off at either end, and so has no connection with the cloaca. In neither genus is there any connection between the testis and the kidney or its duct. The manner in which the sperm is carried to the exterior is now, however, rendered clear in the case of Protopterus, but is not understood in Ceratodus. Günther thought it probable that the sexual products were shed into the body-cavity, and found their way, as in the female, through the open mouths of the ducts, which he designates in the male as "vasa deferentia," and suggested that they were conducted by the longitudinal canal of the testis to certain cavities with thin walls, immediately behind the peritoneum, and thence into the body-cavity. If we suppose that the "longitudinal duct" were to unite posteriorly with the "vas deferens" of Günther, it will be seen that a sperm duct, quite similar to that of Protopterus, would be the result.

It is now well known that in Elasmobranchs and Amphibians, two ducts are early formed in connection with the urinogenital system, and that these are in a certain sense homologous with those in the Amniota. Without going

into special details as regards their development* we know that one of these, the Wolffian duct, functions as the duct of the mesonephros, while the other, or Müllerian duct—the ostium of which in many cases corresponds to part of the pronephros—serves to conduct the ova to the exterior, and becomes more or less completely aborted in the male. In connection with the mesonephros are formed a number of vasa efferentia which serve to connect the tubules of the testis with those of the mesonephros, the duct of which (Wolffian duct) thus becomes a urinogenital duct. The mesonephric tubules are connected with the body-cavity by ciliated funnels, representing (in Elasmobranchs at any rate) the primitive connection between the cavities of the mesoblastic somites and the cœlome proper. With the development of the vasa efferentia, the anterior part of the mesonephros (Urodeles, Elasmobranchs) or the whole of it (Amniota) may give up its primary excretory function, and form the parorchis or epididymis, or the whole may retain its renal functions (Anura). In Urodeles and Elasmobranchs, the renal products are carried off by separate ducts, developed in connection with the Wolffian duct, but opening more or less distinctly from the latter.†

Returning once more to Protopterus, there can be little doubt from a comparison with other Ichthyopsida, that the kidney represents the mesonephros, and its duct appears to correspond with the Wolffian duct;‡

* I will here only refer to a single recent Paper by J. W. van Wijhe on this complicated subject, in which the whole question is fully discussed. It is entitled "Ueber die Mesodermsegmente des Rumpfes und die Entwicklung des Excretionssystem bei Selachien."—Arch. f. mik. Anat., Bd. XXXIII. (*vide* also notes on subsequent page).

† In consequence of this special differentiation of the hinder part of the mesonephros as the persistent urinary organ, it has been supposed by several observers (*e. g.* Balfour) to foreshadow the true hind-kidney or metanephros of the Amniota, and it is therefore sometimes described as a metanephros, and its duct as a ureter (*cf. e. g.* Marshall and Hurst's Practical Zoology"). But as the mode of development of the metanephros appears to differ from that of the mesonephros, no nephrostomes being formed in connection with it, this terminology is perhaps hardly advisable in the present state of our knowledge.

‡ Although the term "Wolffian duct" usually implies a connection with the testis in the male, I use it in preference to "mesonephric duct," for, as van Wijhe has pointed out (*loc. cit.*) this term (or the corresponding word in German—"Urniergang") has a double meaning: it may apply to the unaltered pronephric duct, or to the Wolffian (= secondary mesonephric) duct.

and also that the oviduct, and its representative in the male, is the homologue of the Müllerian duct: the relations of these parts in all the Dipnoi are essentially similar in both sexes to those in the groups mentioned above. The chief divergence consists in the absence of nephrostomes in Protopterus (and probably in the other genera also); but these structures may be modified or reduced in the adult in fishes and Amphibians, and they are almost certainly present in the embryo of the Dipnoi.

The homology of the sperm-duct is, however, not so easy of determination. In my preliminary paper (21) I ventured to suggest that it corresponds to the Wolffian duct; but further reflection, after a more detailed examination of its relations, showed that there are grave difficulties in the acceptance of this view, and that the facts could be explained in another way. If my former supposition were correct, the duct of the kidney must correspond, not to the Wolffian duct itself, but to an offshoot from it, similar to those which conduct the urinary products into the cloaca in Elasmobranchs and Urodeles. The separation between the Müllerian and sperm-ducts in Protopterus is not a complete one, and on this supposed homology, we should have to assume that the former, as in Elasmobranchs, becomes split off from the Wolffian duct, but that the splitting is not complete posteriorly, the two passing into one another shortly before entering the cloaca. There certainly appears to be no reason why this should not be so, for in Elasmobranchs the splitting is not complete, and in the male Chimæra* each Müllerian duct ends blindly on the lateral wall of the elliptical receptacle formed by the union of the two Wolffian ducts posteriorly. The renal duct of Protopterus ought then to open into the common termination of the sperm-duct, and this is not the case. And there are further arguments against this explanation.

In the first place the Wolffian duct, so far as is known, always becomes connected with the testis as well as with the kidney, by means of a rete testis developed in connection with certain of the mesonephric tubules; and the testis, or at any rate that part of it from which the vasa efferentia

* Hyrtl, "Ueb. weibliche Oviducte bei männlichen Chimæren, u. ein männliche Vesicula seminalis beim Weibchen."—Sitzungsberichte d. K. Akad. d. Wissenschaften zu Wien, Bd. x., 1853.

arise, does not then extend along the whole length of the body-cavity. In Protopterus, there are no vasa efferentia, and the testicular tubules are directly connected with the sperm-duct throughout its course along the testis. We should also expect not only that a similar development of Wolffian and Müllerian ducts should take place in Protopterus in both sexes, but that in young females some trace of the former should be found, but this I have not succeeded in doing. If no such rudiment is found—and its presence is very doubtful, for I have examined very small female specimens, not more than half the length of the male in which the Müllerian ducts were distinct—we should have, on the above supposition, to consider that the renal duct was not homologous in the two sexes, although it has precisely similar relations: in the female, it would correspond to the entire Wolffian duct, and in the male only to an offshoot from it. And in both sexes the renal duct opens independently of the generative duct, though enclosed in a common urinogenital sinus in the male. Moreover, Ceratodus stands in the way of this explanation. It seems improbable that the two genera should differ widely as regards the male generative ducts; and the "longitudinal duct" and "vasa efferentia" of Ceratodus would then still remain a riddle.

If we suppose, on the other hand, that the sperm-duct of Protopterus is a special structure, developed in connection with the testis—possibly by the uniting of the testicular tubules into a common collecting duct,—the above difficulties vanish, and it is possible even to give a suggestion with regard to Ceratodus, which further researches must support or condemn.

Apart from the absence of a rete testis in Protopterus, the position of the sperm-duct in both genera, lying, as it does, imbedded within the substance of the testis, strongly militates against its homology with the Wolffian duct. If it is a *special* structure, too, there is no difficulty in accepting the homology of the renal duct in both sexes with the true Wolffian duct. If the sperm-duct is developed in connection with the testis, we should expect that at an early stage it would have no connection with the exterior, and this connection would very probably not take place until towards maturity. According to my observations, the male Protopterus may grow to a considerable size before the sexual products are ripe,

and before the abortion of the Müllerian ducts. Günther's description of the male organs of Ceratodus refers to two males, most of the finer details concerning the smaller specimen, which, although 32 inches long, may possibly, I think, have been immature. The "longitudinal duct" apparently corresponds in position with the sperm-duct of Protopterus, and the "canaliculi seminiferi," as they extend throughout the substance of the testis, and open into the longitudinal duct by innumerable pore-like apertures, may well correspond to the seminal tubules. But Günther does not describe a lobulation of the testis, and the fact that these canals all run parallel to one another, would further indicate that the testis more nearly resembles the simpler anterior than the more complicated posterior part of the gonad of Protopterus. If we suppose that a connection between the blind posterior end of the "longitudinal duct" and the Müllerian duct were to take place by an extension of the former a short distance beyond the testis posteriorly, a sperm-duct quite similar to that of Protopterus would be the result, consisting of an anterior part extending throughout the testis and for a short distance beyond it, and of a short posterior part, corresponding to the posterior end of the Müllerian duct. No explanation, however, would be given of the cavities below the peritoneum described by Günther, which, on injection, appeared to communicate with the seminal duct. It is quite possible, however, that owing to the state of preservation of the specimen, this connection was only an artificial one.*

As the structure of the female generative ducts in the Dipnoi is in many

* In a recent Paper by Hector F. E. Jungersen ("Beiträge zur Kenntniss der Entwickelung der Knockenfischen,"—Arbeit. aus dem zool. zoot. Inst. in Würzburg, Bd. IX., 1889), the author criticises the homologies of the male generative ducts of Protopterus suggested in my preliminary Paper, and gives a similar explanation to that at which I had since arrived. He finds that in Teleostei the free independent portions of the generative ducts arise after the sexual differentiation of the gonads, and, like the latter, are formed as special developments of the ridges of peritoneal epithelium which form an immediate continuation of the genital folds. The duct of the testis always forms a direct continuation of the gonad, while that of the ovary is temporarily or permanently independent of the gonad. The oviduct of Teleosteans, and probably of Ganoids also, may thus be called a Müllerian duct only in so far as it is developed from the peritoneal epithelium.

respects so similar to that of Amphibians, and to a less extent to that of Elasmobranchs and Chimæroids, it is certainly curious to find that the male generative duct should have such a special character, which has, perhaps, its nearest analogy in Teleosteans. In these fishes the generative ducts are, however, apparently special structures in *both* sexes, developed quite independently of the primitive excretory system, so that here there is neither Wolffian nor Müllerian duct—at any rate in the sense in which these terms are used with regard to Elasmobranchs. It seems very doubtful, also, whether a true Müllerian duct is developed amongst Ganoids,* and certain observations with regard to the connection of the testis with the renal duct by means of vasa efferentia in the Sturgeon † and in Lepidosteus, ‡ seeming to indicate that the testicular products may pass out through the unsplit pronephric duct, perhaps require confirmation.§

There appears to be little reason for supposing that the urinogenital organs of Elasmobranchs present a very primitive condition,‖ and if, as seems most probable, the ancestors of existing Vertebrates were hermaphrodite,¶ there is no reason why arrangements for the prevention of self-fertilization should not have become developed on different lines in the various groups. In its mode of development, the Müllerian duct does not seem to be strictly homologous in the Elasmobranchii and Urodela on the one hand and the Anura and Amniota on the other, as in many instances, at any rate, it arises independently of the Wolffian duct and pronephros in

* *Cf.* Brock, Zeitschr. f. wiss. Zool. Bd. XLIV., p. 375; Beard, Anat. Anz., 1890, pp. 14–22.

† Rathke, "Ueb. d. Geschlechtstheile d. Fische," Neueste Schriften d. naturforsch. Gesellsch. in Danzig, Bd. I., Heft 3, Halle 1884; and "Zur Anat. d. Fische," Müller's Archiv, 1836; Wiedersheim, Lehrbuch d. vergl. Anat., 2te Aufl. 1886, p. 773, fig. 582.

‡ Balfour and Parker, Phil. Trans., 1882.

§ Jungersen (*loc. cit.*) throws much doubt on these observations, and his description of Acipenser (p. 187) seems to show that there may be a close resemblance between this Ganoid and Protopterus as regards the formation of the male generative ducts.

Since the above was written, R. Semon ("Notizen üb. d. Zusammenhang d. Harn- u. Geschlechtsorgane b. d. Ganoiden"; Morph. Jahrb., Bd. XVII., Heft 4, Oct. 1891) has fully confirmed the results obtained by Balfour and myself with regard to the connection between the testis and kidney in Lepidosteus.

‖ *Cf.* Balfour, "Urinogenital Organs of Vertebrates," Mem. Ed. p. 153.

¶ *Cf.* van Wijhe (*loc. cit.*).

the two last-mentioned groups.* And although, perhaps, the oviduct of Teleosteans (and Ganoids) may be in a sense partially comparable (*cf. supra*), to that of the Anura and Amniota, in many respects its formation is very dissimilar. The sperm may, moreover, be conducted to the exterior by means of the primary (?) (Acipenser, Lepidosteus) or secondary (Elasmobranchii, Amphibia, Amniota) mesonephric ducts, or by ducts specially developed for this purpose (Teleostei, ? Dipnoi). In some Vertebrates, again, no ducts at all are present in either sex (Marsipobranchii, and in the females of certain Teleostei), sexual differentiation of the gonads having here probably taken place † at a relatively earlier period than in other Vertebrates, in which this differentiation may have occurred *after* the specialization of male and female generative ducts ‡ (van Wijhe).

The Torpid State of Protopterus.

The first account of the peculiar manner in which Protopterus passes the dry season was given by Sir William Jardine in 1841 (13), who, on the authority of a Miss Weir, states that it only spends about three months of the year in the water; for the remaining nine months the water is dried up, and the substratum becomes dry and hard. On the approach of the dry season the animals burrow into the earth,§ and at about 18 inches,‖ from

* *Cf.* (*e. g.*) Marshall and Bles (*loc. cit.*), and Wiedersheim, "Ueb. die Entwick. des Urogenitalapparates bei Crocodilien und Schildkröten"—Arch. f. Mik. Anat. Bd. xxxvi., 1890.

† Except in Myxine, which has apparently retained the hermaphrodite condition.—(J. T. Cunningham, Trans. R. Soc. Edin., 1886. Nansen, Bergens Mus. Aarber., 1887).

‡ Jungersen (*loc. cit.*) shows that in the Teleostei, in which the excretory system takes no part in the formation of the generative ducts, sexual differentiation does generally occur before the latter are developed. In a Paper recently read before the Linnean Society, Howes has put forward the view that the generative duct in Ganoids and Teleosts represents the primary (? hermaphrodite) duct, the specialization of Wolffian and Müllerian ducts being associated with the first step towards unisexuality (Linn. Soc. Journal, Zool., vol. xxiii., 1891). I might add that Chrysophrys and Serranus are not only always hermaphrodite, but that the latter is said to be self-impregnating.

§ The thick lips are probably specially adapted for burrowing, and the position of the anterior nostrils must also be advantageous to the animal in this process.

‖ 40–50 Ctm., Stuhlmann (25).

the surface, coil themselves up, each becoming surrounded with a membranous "cocoon" or capsule, a rough figure of which is given by Jardine.

Gray (6), quoting a Dr. Daniel, states that Protopterus is only found in the rice-fields, which are more than half a year under water, and that it is only procured by the natives towards the end of the dry season, when it is dug out of the nearly dried mud. M'Donnell (18) mentions that it lies buried for 4 to 7 months. More recently Stuhlmann (25) has shown that the free life of the animal, including the period of reproduction, extends from January to July in each year, the period naturally varying somewhat with the seasons. This refers to Quelimane; in Senegambia, Ayers (1) states that the breeding time is in August.

Peters (14) and Bartlett (quoted by Gray, 6) imagined that the capsule was composed of dry leaves, but the subsequent statement of Krauss (16) and Paulson (23), * that it is produced from the hardened mucus secreted by the animal, has recently been fully confirmed by Wiedersheim (30), who has shown that it is formed as a secretion of the abundant integumentary glands which becomes hardened where it comes into contact with the surrounding earthy mass, † and which (as an analysis of the capsule since made by Walther (27) shows) becomes impregnated with substances derived from the latter. The outer surface of the cocoon shows the impression of the roots of plants, many of which, as well as particles of earth, remain adhering to it (Pl. XVII., fig. 68).

The burrow has been compared to a mouse's hole, and is closed below by the upper end of the capsule. Within the latter, the animal lies coiled up (fig. 67) in such a manner that the head lies alongside the base of the tail, which from this point is again bent backwards over the head, so that it covers the head and body like a veil. The extremities lie quite close to the body, and are, more particularly in the case of the pectoral fin, bent into a flat spiral, the apices of the pelvic fins projecting between the snout

* *Cf.* also M'Donnell (18), who compared it to a "slough."

† Stuhlmann states that if a portion of the capsule is broken away, the mucus again hardens over the broken place to form a thin membrane.

and the base of the tail anteriorly.* The end of the tail is usually curved dorsalwards † to a greater extent than is shown in fig. 67.

Between the capsule and the body of the animal is a slimy mass of the consistency of varnish, which can be drawn out into threads (30). This substance is a mucus, secreted by the integumentary glands, its function without doubt being to keep the integument moist, as well as to form the capsule by a hardening of its peripheral part. The presence of this mucus renders possible the existence of the sense-organs in the integument during the torpid state, for it is well-known that all such sensory cells require a fluid medium.

It is naturally impossible to say whether the multicellular glands take any important part in forming the slimy secretion and the capsule, but the far greater abundance of goblet-cells leaves little doubt that these must be the chief mucus-secreting agents.

The capsule (fig. 68) has a pitcher-like form ;‡ it is rounded off below, and then narrows somewhat towards the upper end, which is closed by a sort of convex lid, against the inner concave side of which the snout of the animal presses (figs. 67–69). The lid is doubtless broken through at the margins when the animal frees itself, and in dry specimens of the cocoon this is often indicated by a more or less complete split between the lid and the pitcher. The position of the mouth can easily be seen from the outer convex side of the lid which closes the bottom of the burrow as a transverse groove extending tangentially across it (fig. 69). In the centre of this groove a small aperture can be recognised, and a careful examination

* In Wiedersheim's figure of the encapsuled animal (30) the appendages are wrongly lettered ; those which are marked "pectoral" are the pelvic fins, and *vice versa*.

† Stuhlmann also noticed this upward bend of the apex of the tail. (*Cf.* p. 118.)

‡ Besides Jardine's figure, an outline of the capsule is given by Gray, who shows a band extending across its interior, through the angle between the body and tail: this I have not observed. Woodcuts of the encapsuled animal were also given recently by O. Zacharias, in a popular article in the Leipziger illustrirter Zeitung, p. 350, Bd. xcr., Oct. 6, 1888. M'Donnell and Wiedersheim have figured the coiled-up animal after removal from the cocoon. Stuhlmann states that the cocoon-membrane is formed in all portions of the body, not only in the position of the cocoon-wall, but also on the extremities, the margins of the lips, and even in places where two portions of the skin come into apposition.

of the relations of the animal *in situ* show that the margins of the aperture are produced inwards to form a funnel-shaped tube or pipe, lying between the lips of the animal so as to reach the anterior nostrils, and doubtless produced by suction before the hardening of the capsule. In this way a free passage is left for the respiratory current. Bubbles of air were always given off from the lungs when the animals were removed from the cocoon and placed in water.

This aperture was noticed by Jardine and Bartlett, although they did not describe its exact relations to the mouth (*cf.* 21). More recently Stuhlmann states that the aperture was quite as often absent as present, and that he only found the tube in one case out of about twenty. But he mentions that in many instances the capsules had been disturbed during the process of digging them out, and this may account not only for his having overlooked the tube, which is not always easy to make out unless the cocoon is removed very carefully, but also for his statement that a split is sometimes present between the lid and the body of the cocoon for the entrance of air, and that even the lid is not always present.*

Wiedersheim noticed a distinct reddening of the tail of the animal when it was removed from the cocoon, which (as in the one or two specimens he then had at his disposal he did not observe the pipe) led him to believe that respiration takes places during the torpid period by means of the caudal blood-vessels. But even if the mode of respiration could not be more easily explained—I mean by the direct access of air to the lungs—it is not easy to understand how the air could come into relation with the blood-vessels of the tail. In the first place the dense mass of earth surrounding the capsule would probably not contain a sufficient supply of fresh air for this purpose, and one does not see how, even supposing this to be the case, it would be possible for osmosis to take place through the cocoon membrane and the mass of mucus lying between the

* Stuhlmann has misunderstood my former account of the lid. I compared it to the tympanic membrane only as regards its general concavo-convex form. Its relations to the earthy tube are not similar to those existing between the tympanic membrane and the meatus. I notice that R. Burckhardt (Sitzungsber. d. Gesellsch. naturforsh. Freunde zu Berlin, Oct. 21, 1890) has recently found the "pipe" in nearly all the examples he examined.

latter and the body. At the same time, there is no doubt that the integument of the sleeping animal does often show the red colour which led Wiedersheim to the above conclusion; and this, as Stuhlmann has since stated, may be sometimes—but by no means always—seen not only on the tail, but also on other parts of the body. It is possible, as the last-mentioned observer suggests, that the colour may be due to a rich vascularisation of the skin, which is most apparent in parts where the pigment is less abundant, and which is connected with the greater activity of the skin in producing mucus during the torpid state.

A yellowish substance could usually be seen in the neighbourhood of the vent when the animal was removed from the cocoon, but I can state nothing as to its nature. Stuhlmann observed no excrement, but only a clear fluid in this position, which, like the mucus, could be drawn out into threads.

The observations of Stuhlmann showing that it is possible to induce the torpid state artificially by putting fine earth into the water, so as gradually to reduce its depth, are worthy of note.

The sounds which Protopterus make on being released from its capsule are very peculiar, and have been noticed by several observers. M'Donnell * speaks of it as a "squeak" and Bischoff mentions that Lepidosiren produces a sound like that of the cat. Natterer also refers to the voice of the last-named species, and Günther states that Ceratodus † is said to make a grunting noise. Krauss mentions that Protopterus also gives out a curious sound after having come to the surface to take in air. There certainly

* M'Donnell states that the animal was not heard to produce any vocal sound after having been placed in water. On being taken out of the water occasionally, it made no other sound than a "smacking," like that produced by eels and other fishes (*cf.* Joh. Müller, "Ueb. die Fische, welche Töne von sich geben und die Enstehung dieser Töne."—Müller's Archiv, 1857).

† Very little seems to be known about the habits of Ceratodus. It is said to come temporarily out of the water (*vide* Krefft, Proc. Zool. Soc., 1870, p. 221); but E. S. Hill, in a note quoted by Günther (7), throws doubt on this statement. (*Cf.* also E. P. Ramsay, Proc. Zool. Soc., 1871, p. 7, and J. Baldwin Spencer, "Nature," July 28, vol. xlvi., 1892.) Macleay (Proc. Linn. Soc. N. S. Wales, p. 211, vol. xviii., 1884, and Zoologist, 3rd series, vol. vii., 1883) mentions that Ceratodus makes slight indentations in the muddy bottom in which the spawn is deposited, and that the spawn resembles that of the frog.

is a difference between the sound made before, and after, the animal is placed in the water. In both cases it somewhat resembles a smacking of the lips, but in the former case it has more the character of a true vocal tone: this may, however, be simply due to the fact that the mouth and lips are only moistened by mucus, and not by water. Not only from the nature of the sound, but also from the fact of the absence of any proper laryngeal apparatus, I am inclined to believe that the sound is always produced simply by the sudden forcing of a current of air out of the lungs between the lips.

One of the most interesting points which presents itself with regard to the life of Protopterus is the question as to its nutrition during the summer sleep. As already mentioned, a considerable quantity of fat becomes deposited on the investing tissue of the gonads and kidneys, and moreover, a dissection or section of the base of the tail reveals the fact that large tracts of adipose tissue are present amongst the lateral muscles along the spinal axis in this region,* extending from the hinder end of the body for some distance into the tail (Pl. vii., fig. 1, and Pl. x., fig. 22).

As my specimens were examined in July, it is probable that they had been torpid for some months, at any rate. But they all appeared well nourished, and much fat was contained in the tissues above referred to. Stuhlmann's observations in this respect are quite similar to my own. But in order to obtain accurate statistics as to the deposition and absorption of fat, it would be necessary to examine specimens just before, and just after the torpid period. There can be little doubt, however, that the fat, like that in the corpora adiposa of Amphibians, and the "hibernating gland" of certain Rodents, serves as a store of nutriment for the sleeping animal.

The presence of such considerable fatty tracts in the tail at once arrested my attention, and dissections and sections plainly indicated that the muscular tissue in these regions had apparently been replaced by fat, and that in many places the perimysium enclosed nothing but fat, while in others, some of the muscles had undergone considerable change as regards their histological structure.

These appearances naturally called to mind the researches of Miescher

* This fact was noticed by M'Donnell (18).

Rüsch and others * with regard to the mode of nutrition of the Salmon during the breeding season. It appears that this fish takes no food during this period and for some time previously, although the generative organs develope considerably.†

A somewhat similar phenomenon also occurs, according to Schneider,‡ in the Lamprey, in which, however, the degeneration does not appear to be of a fatty nature. Schneider says: "Wenn *Petromyzon fluviatilis* nahe dem Laichen ist, degeneriren die Muskelplatten zum grossen Theil, während die parietalen Primitivbündel unverändert bleiben. Die fibrillare Structur geht unter, die Platten fliessen zusammen und sind in eine feinkörnige, wie Eiweiss-aussehende Substanz verwandelt, welche viele grosse Kerne einschliesst. Aehnliche Veränderung der Muskelsubstanz haben Virchow bei der Trichinose (1860), C. O. Weber nach Verwundung, Zenker beim Typhus nachgewiesen. Diese Degeneration bewirkt wahrscheinlich die Mattigkeit, welche A. Müller an Petromyzon nach dem Laichen beobachtete."

A degeneration apparently very similar to that described by Schneider in the case of the Lamprey is seen in certain parts of the muscles of Protopterus referred to above, interposed amongst, and surrounding the fatty portions externally. This is at once indicated in stained preparations by the degenerated portions appearing lighter in colour than the rest. Examination under a high power shows that in these regions the muscles have to a greater or less extent lost their characteristic structure. The fibrillation and transverse striation can no longer be seen in parts of the fibres, and more or less of the contents of the sarcolemma sheath is seen to be filled with a coarsely granular substance (Pl. x., figs. 23 and 24). Professor Ziegler, to whom I showed my preparations, informed me that the appearance presented was quite similar to that seen in the ordinary pathological degeneration of muscular fibres.

* *Cf.* Miescher Rüsch, "Ueb. das Leben des Rheinlachses im Süsswasser," Arch. f. Anat. u. Physiol., 1881; D. Barfurth, "Der Hunger als fordendes Princip in der Natur," Arch. f. mik. Anat. Bd. xxix., 1887; and the literature given by these authors.

† It is interesting to compare this period of hunger with that of hibernating animals. The dormouse is said to gain weight during its fast (*vide* Foster's Physiology, p. 82, *et seq.*).

‡ Beiträge zur vergl. Anat. u. Entwickelungsgeschichte d. Wirbelthiere, Berlin, 1879.

Longitudinal sections (fig. 23) and teased-out preparations show still more clearly than transverse sections (fig. 24), that this disintegration occurs in small islands in a muscular fibre, and then spreads, so as to gradually replace more and more of the normal contractile substance, and at the same time shrinkage from the sarcolemma occurs, which may, however, possibly be due to the action of the reagents.* There appears to be first a fibrillar degeneration, causing a loosening of the muscular substance, followed by a granular degeneration with the formation of vacuoles. I noticed no degenerative changes in the nuclei. It is very possible that this granular degeneration is a precursor of the fatty degeneration; but after several attempts, and treatment with osmic acid and other reagents, I have not succeeded in observing the actual formation of fat in the fibres, or any indication of intermediate stages between the granular and the fatty tissue.

Although all these points require further investigation, there can be little doubt that the lateral muscles of Protopterus, as well as the fat in the lymphoid tissue† investing the urinogenital organs, serve as a store of nutriment for the animal during the torpid state; and, as in the case of the Salmon and Lamprey, are important, not only in supporting its life, but also in supplying material for the formation of the generative products, which are extruded shortly after the animal wakes from its sleep. The statement of the negroes, quoted by Stuhlmann, that during the torpid period Protopterus consumes its own tail, is not, therefore, such a fable as it would at first appear.

* I should add that these degenerative changes could be seen in *all* my preparations, whether preserved in alcohol, chromic acid, corrosive sublimate, or aceto-osmio-chromic acid.

† I am not aware whether any observations have been recorded which show the actual transformation of lymphoid into fatty tissue. Professor Ziegler, however, informs me that the marrow of the bones is of a lymphoid nature at first, and later becomes transformed into adipose tissue—either partially, as in the sternum and epiphyses, or entirely, as in the diaphyses of the long bones; and also that in pathological cases, *e. g.* in *anæmia perniciosa*, fatty marrow may become transformed into entirely lymphoid red or grey marrow: it is quite possible that a metamorphosis in the reverse direction may occur. It is known, moreover, that lymphatic glands may, during atrophy, become transformed into fatty tissue, the leucocytes disappearing, and the fixed cells giving rise to fat cells. But this process only appears to take place occasionally, as in *marasmus senilis*.

The feebleness noticed by Müller in Petromyzon after deposition of the sexual products on account of the degeneration of its muscles, is not observable in Protopterus after many months of torpor (p. 111 *et seq.*). The fact that the Lamprey dies soon after the first oviposition probably accounts for this difference.*

The problem also still remains as to how all the degenerated material becomes absorbed and passed into the blood, so as to be carried to the various parts of the body.

It is well known that certain of the tissues in insect larvæ serve as nutrient material for the building up of the organs of the adult.† In this process it appears that the tissues undergo "histiolysis," are ingested by the amœboid blood-corpuscles, and thus become transferred to other regions of the body. The importance of leucocytes in absorbing and distributing food material is probably considerable in most Invertebrates, and there can be little doubt that they also have a similar function to a greater or less extent in Vertebrates, although our knowledge in this respect is still very vague.

The question as to the part played by leucocytes in the ordinary processes of the digestion of food in the alimentary canal of Vertebrates has already been briefly touched upon, and I will here only call attention to the researches of Metschnikoff‡ and Barfurth,§ with regard to the

* Panizza, "Memoria sulla lampreda marina," Memorie dell' Institute di Scienze, vol. II., Milan, 1845; A. Müller, "Vorläuf. Ber. ueb. d. Entwick. der Neunaugen," Müller's Archiv, 1856; Von Siebold, "Die Süsswasserfische Mitteleuropa's." *Vide* note on p. 482 of a Paper by Jacoby, "The Eel Question," Rep. U. S. Fish Comm. for 1879, Part VII., Washington, 1882.

This fact is indicated by the structure of the alimentary canal and the degeneration of the liver and bile-duct which occurs at metamorphosis.

† *Cf. e. g.* A. Weismann, "Die Entwick. der Dipteren," Zeitschrift f. wiss. Zool. Bd. XIII., 1863; Kowalewsky, "Beiträge zur nachembryonal. Entwick. der Musciden," Zool. Anz., Jahrgang 8, 1885; and J. van Rees, "Beitrag zur Kenntniss der inneren Metamorphose von *Musca vomitoria*," Zool. Jahrbücher, Abtheil, f. Anat. u. Ontogenie d. Thiere, Bd. III., 1888.

‡ "Untersuch. üb die mesodermalen Phagocyten einiger Wirbelthiere," Biol. Centralblatt, Bd. III.

§ "Die Rückbildung des Froschlarvenschwanz, u. die sogennanten 'Sarcoplasten,'" Arch. f. mik. Anat. Bd. XXIX., 1886; *cf.* also Sigismund Mayer, "Studien zur Histol. u. Physiol. des Blutgefässsystems," Anzeiger d. K. Akad. d. Wissenschaften, XIX. Jahrgang, Wien, 1882.

metamorphosis of the tadpole. These show that the tail serves as nutrient material during metamorphosis, its tissues undergoing histiolysis and then being transported into the lymphatic trunks of other parts of the body by wandering leucocytes, there to be used up in the formation of the new tissues. In this process, the muscle-fibres undergo fatty degeneration, and break up into "sarcolytes." The degenerated material is said then to be taken up by the leucocytes and thus passed into the lymph-trunks. It is very probable that the absorption of the degenerated muscular tissue in the Lamprey, Salmon, and Protopterus takes place in a similar manner, but to this I will return presently.

In a recent Paper, Loos * states his opinion that Metschnikoff's conclusions with regard to the absorption of the tail in the Frog-tadpole have been given too wide a bearing, for the leucocytes play a much less important part in this process than in the Diptera and in Invertebrates generally; and it is evident that more observations are required on this point before we can arrive at any very definite conclusions on the matter. Loos states that "the leucocytes would seem to form a kind of reserve force for the animal body, which only comes into prominent use if the organism is unable, with the ordinary means at its disposal, to perform certain extraordinary duties, or to struggle against difficult relations."

In my preliminary Paper on Protopterus (21) I made the following statements with regard to the absorption of the muscular tissue:—"Die Leukocyten und wohl auch die neuerdings von P. Poljakoff beschriebenen amoeboiden Bindegewebskörper wandern ein, reissen das zerfallende und verfettende Muskelgewebe an sich und begeben sich damit auf die Wanderschaft. Die Uebereinstimmung des Leukocyten-Inhaltes mit den im Perimysium zurückbleibenden Gewebsresten ist auf Schnitten deutlich nachzuweisen. Bemerkenswerth ist dabei der Umstand, dass der Muskel in vielen Perimysialfeldern gänzlich jener Metamorphose zu verfallen scheint, während an anderen Stellen histologisch intacte Muskelreste sich erhalten, welche nach dem Sommerschlaf offenbar zur Regeneration verwendet werden."

* Biol. Centralblatt, IX., 1889. Quoted from abstract in the Jour. Roy. Micros. Soc., 1890, p. 158, part II.

To these conclusions I was led by certain appearances presented in my serial sections of a small specimen. Not only could certain cells, which had all the appearance of leucocytes, be seen amongst the degenerating muscular tissue, but certain of these, in various parts of the body, were seen to contain particles which resembled the remains of the degenerating muscle. But this conclusion has received no support from my subsequent observations, and although I still think it probable that the leucocytes are the transporting agents, I am unable to add any further proof beyond what has already been stated with regard to the degenerating muscle and the peculiar regressive changes observed in certain of the leucocytes of the blood. The particles which I took to be the remains of the muscular tissue within the leucocytes are, as already mentioned, to be seen in cells in various parts of the body (around the ovaries, kidneys, intestine, etc.); but in the sections above referred to they are most apparent in some lymphoid tissue at the base of the lung, and it is very likely that in this case they are simply foreign particles of inorganic or organic matter—possibly Bacteria—which had found their way into the lungs with the respiratory current, and had then been ingested by the leucocytes, just as occurs in cases of siderosis and anthracosis. Possibly also, they may simply be leucocytes of form B, the contents of which are peculiarly stained. The appearances in the leucocytes in the walls of the intestine may be explained in a similar manner, and those in the amœboid cells of other parts of the body may be due to their having wandered into these places after having absorbed the particles from the lungs or gut. On the other hand, my earliest explanation may be the true one; but before any definite conclusions can be arrived at, it will be necessary to follow out carefully the details of the whole process of degeneration and absorption, and to make comparisons between torpid specimens and those which have been active and well nourished for some time after leaving the cocoon. It would then, perhaps, be possible to get an explanation of the manner in which the muscular tissue becomes regenerated, about which I have nothing to add to the somewhat vague and possibly incorrect statement quoted above. That Protopterus has great powers of regeneration of

its tissues is indicated by the observations with regard to the restoration of the tail and fins already referred to.*

Addendum.

As it is known that the muscles and other organs of Elasmobranchs retain considerable quantities of the products of nitrogenous excretion,† while these are absent in the muscles of most other Vertebrates, and, in fact, act as a poison, it seemed worth while to make an examination of Protopterus with regard to this point.

Professor Baumann was good enough to make the following analysis for which, as well as for that of the contents of the gut, I offer him my best thanks. I should state that the specimen used had been active for some weeks.

"Da es zunächst darauf ankam festzustellen, ob in den Muskeln des Lungenfisches erhebliche Mengen von Harnstoff oder Ablagerungen von Harnsäure bez. harnsauren-Salzen and verwandten Körpern vorkommen, wurde mit 100 Gramm der Muskeln eine qualitative Prüfung vorgenommen.

"Die von den Knochen nicht getrennten Muskeln wurden zerkleinert und mit absolutem Alkohol in der Wärme extrahirt. Die weingeistigen Auszüge wurden verdunstet, der Rückstand in Wasser gelöst und filtrirt. Nach dem Einengen der wässrigen Lösung kristallisirte eine kleine Menge Kreatin aus. Die davon abgezogene Mutterlauge wurde mit saltpetersaurem Quecksilberoxyd gefüllt, der dabei gebildete weisse Niederschlag wurde abfiltrirt, in Wasser zertheilt, und mit Schwefelwasserstoff zerlegt. Die vom Schwefelquecksilber abfiltrirte Lösung wurde wieder verdunstet und zur Kristallisation gestellt. Dabei wurden keine Kristalle von saltpetersaurem Harnstoff gebildet, selbst nicht nach Zusatz einiger Tropfen concentrirter Saltpetersäure.

* An important Paper by Barfurth, "Zur Regeneration der Gewebe," has appeared since the above was written (Arch. f. mik. Anat. Bd. xxxvii., 1891).

† C. Fr. W. Krukenberg, "Die Harnstoffretention in den Organen der Rochen u. Haie." Centralblatt f. d. medicinischen Wissenschaften, No. 25, 1887.

"Es könnten somit höchstens Spuren von Harnstoff in den untersuchten Muskeln enthalten sein, dessen Fortsetzung desshalb nicht weiter versucht wurde.

"Die mit Alkohol extrahirten zerkleinerten Muskeln wurden zur Prüfung auf Harnsäure mit heissem Wasser ausgezogen. Die wässrigen Auszüge wurden, bis ihr Volumen noch 25 c.cm. betrug, verdunstet und mit einiger c.cm. verdünnter Salzsäure versetzt. Auch nach längerem Stehen wurde aus dem angesäuerten Extrakte keine Abscheidung von Harnsäure erzielt. Die saure Flüssigkeit gab mit ammoniakalischer Silberlösung eine mässige Trübung von dem Niederschlage der Silberverbindungen Xanthin-Körper, welche somit jedenfalls auch nicht in einer abnorm vermehrten Menge zugegen waren."

General Abstract, Summary of Chief Results, and Conclusions.

1. A general account of the habits of Protopterus is given (pp. 111–114).

2. The paired extremities, although their movements are more like those of limbs than of fins, show no connection with the cheiropterygium, and are evidently, in spite of their considerable nerve supply, greatly degenerated structures as regards their free portions. Sensory organs are absent on them, and they therefore cannot have a tactile function. The tail is almost certainly not primarily diphycercal; its apex, like the distal ends of the paired fins, is very variable, and shows signs of reduction (pp. 115–118, and figs. 1 and 67).

3. The epidermis, though intermediate in character between that of fishes and that of Amphibians, on the whole most nearly resembles that of the Perennibranchiata. As in Amphibians, it gives rise to simple multicellular glands, which are most numerous on the snout. A very marked character is seen in the great abundance of goblet-cells (*cf.* paragraph 30 of this abstract). The epidermis forms a regular and continuous layer over the derma, in which the imbricating cycloid scales are imbedded. Pigment cells are present in both layers of the integument. The derma encloses

nests of leucocytes here and there, and small cells, apparently migratory leucocytes, can be seen in places in the epidermis (pp. 118–121, and figs. 2, 8–22, 36, 37, and 38).

4. Integumentary sense-organs, similar to those of fishes and larval or perennibranchiate Amphibians, are present not only on the head and along the lateral line, but in various other parts of the body, and are most numerous on the head. Primarily they are all superficial, and do not project below the level of the epidermis, and this condition is retained in those situated on the trunk. On the head, however, the epidermis becomes involuted along certain lines to form grooves, which, by the joining of their margins, become converted into sub-epidermic tubes, in which the sensory organs are situated, and which communicate with the exterior by an aperture at one end. The relations of the sensory organs of the trunk therefore resembles those seen in young stages of most fishes and Amphibian larvæ, while in the case of the head, they are similar to those which are typical for adult fishes (pp. 121–123, and figs. 8–22, 37, 38, and 70).

5. End-buds, similar in structure to the taste-buds of fishes and Amphibians, are present on the tongue and oral epithelium, but are absent on the lips and apparently also on the surface of the body, as in Amphibians and the higher Vertebrates (pp. 123 and 124, and fig. 3).

6. The olfactory organ most nearly resembles that of Elasmobranchs as regards its general structure, but the presence of posterior nostrils raises it to a higher level. The position of the anterior nostrils beneath the upper lip is probably to be accounted for as an adaptation in connection with the torpid state (*vide* paragraph 30). No special glandular apparatus is present in connection with the nose (pp. 124–126, and figs. 9–13, 25 and 26).

7. The space between the eye-ball and its muscles, and the orbit, is filled by a delicate connective tissue; there are no orbital glands or eye-lids. Four straight and two oblique muscles are present. The cornea is continuous with the derma on the one hand, and the sclerotic on the other. The latter is fibrous in young individuals, and islands of cartilage first appear at the points of insertion of the eye-muscles, and then gradually extend so as to chondrify the whole sclerotic. The general structure of the

eye on the whole closely resembles that seen in Amphibians: a *processus falciformis* and a *campanula Halleri* are not present, and no ciliary muscles were recognised, though possibly present. Almost all the pigment of the eye is ectodermic (pp. 127–129, and figs. 14 and 15).

8. The oral epithelium is essentially similar in structure to the epidermis, but is much folded, so as to give rise to the appearance of a number of close-set, simple glands; no specialized glands are, however, present in connection with the mouth cavity. The lips contain no muscles. The tongue, as well as the palate, is covered with blunt, conical papillæ, on which the taste-buds are situated. Beneath the epithelium, the tongue is composed, anteriorly to the hyoid, of a simple connective tissue, like that of the lips; while posteriorly to the hyoid it is made up of extrinsic muscles in connection with the visceral apparatus, the main mass of which is continuous with the ventral musculature of the trunk (pp. 129–131, and figs. 8–16 and 27).

9. A horny cap is developed over each tooth from the overlying epithelium, which apparently becomes cut through by the sharp edges and points of the teeth, and probably corresponds to the *cuticula dentis*. Indications of the enamel epithelium could be recognised (pp. 131–134, and figs. 4 and 11–13).

10. The thyroid is a small bilobed organ imbedded in the tongue just above the hyoid symphysis, and has the characteristic structure. The thymus consists of lymphoid tissue, and is situated dorsally and posterior to the branchial arches. It is divided into an internal and an external lobe, and surrounds the blood-vessels of the external gills (pp. 135, 136, and figs. 1, 15, 16, 20, 27, 27A.).

11. The alimentary canal extends almost in a straight line from the mouth to the vent. The œsophagus passes insensibly into the stomach, and both have very thin walls. The thick-walled intestine is provided with a ventral, as well as a fenestrated dorsal mesentery. The form of the spiral valve is very similar to that of Scyllium. The so-called "urinary bladder" (cloacal cæcum) opens into the cloaca dorsally to the intestine. It may possibly be compared with the *processus digitiformis* of Elasmobranchs (pp. 136, 137, 140–142, and figs. 1, 21, 28–34 and 54).

12. A distinct pancreas is present, the relations of which are somewhat similar to those seen amongst Ganoids and in certain Teleosteans. It is embedded in the walls of the *bursa entiana* and stomach, and is deeply pigmented; its position can only be seen externally by the dark colour of the walls of the gut in this region. It is covered externally by sparse muscular fibres as well as by the thick peritoneun of the gut. The pancreatic ducts unite with the bile duct shortly before the latter penetrates the walls of the intestine (pp. 138, 139, 148, and figs. 29, 31 and 32).

13. A very marked character of the alimentary canal is the great abundance of lymphoid tissue in connection with it. A large lymphoid organ, which corresponds to the spleen, is imbedded in the walls of the stomach, extending backwards on to the anterior part of the intestine so as to partially overlie the pancreas; like the latter, it is covered externally by muscular fibres and peritoneum. In the intestine, masses of lymphoid tissue make up the greater part of the thickness of the spiral valve as well as of the outer wall. The spleen, pancreas, and internal lymphoid organ thus appear like differentiations of a continuous band of tissue in the wall of the gut (pp. 138–141, 145, 147, and figs. 1, 6, 7, 21, 28, 29, 30–34, 40, 43).

14. With the exception of the *bursa entiana* [on p. 141, line 6 from bottom, "*spiral valve*" should read "*bursa entiana*"], the internal walls of which are raised up into a number of deeply pigmented oblique folds, the whole of the mucous membrane lining the stomach and intestine is perfectly smooth. That of the œsophagus and rectum can be thrown into temporary longitudinal folds on contraction (pp. 140, 141, 144, 157, and figs. 28, 30–34, 54).

15. Cilia are present on the epithelium throughout the stomach and intestine, and a further very primitive character is seen in the absence of any differentiated gastric or intestinal glands. The epithelium is columnar and stratified, and goblet-cells are abundant. Branched pigment-cells extend into the epithelium in the greater part of the intestine, and small leucocytes could be seen amongst the epithelial cells here and there. A layer of small-celled lymphoid tissue directly underlies the epithelium (pp. 143–145, and 149–153, and figs. 5, 30–34, 39, 42, 43 and 63).

16. In the lymphoid organs of the gut (including the spleen) two kinds of tissue can be distinguished, (1) a large-celled tissue, which forms the greater part of these organs, and which somewhat resembles embryonic connective tissue, and (2) groups or masses of a smaller celled tissue, similar to that lying directly beneath the epithelium, and resembling that of ordinary lymphoid follicles. Large migratory leucocytes are present in both kinds of tissue, many of which enclose yellowish granules. Gradations between these and rounded cells of a deeper yellow or brown colour can apparently be made out:—the latter are arranged in larger or smaller groups, and cells appearing to be intermediate forms between them and the ordinary branched black pigment cells can also be seen. The lymphoid tissue is penetrated by networks of blood-vessels, and it seems probable that the yellow granules mentioned above are due to the disintegration of red corpuscles, which are ingested by leucocytes, and then undergo some change whereby the leucocytes gradually give rise to black pigment-cells which migrate through the epithelium and are so got rid of (pp. 145, 146, 154–156, and figs. 6, 7, 30–34, 37, 40, 42, and 43).

17. The muscular layers of the alimentary canal have a rudimentary appearance. A *musculus mucosæ* is present, and the circular and longitudinal layers are represented, but the direction of the fibres is in many regions difficult to trace. Strands, only a few cells in thickness, extend throughout the lymphoid tissue of the intestine, and some of these unite to form a longitudinal band passing down the axis of the spiral valve (pp. 146–148, 153, and figs. 30–34, 42 and 43).

18. An analysis of the contents of the gut, while yielding negative results as regards the stomach, proves the presence of peptones, in very small quantities, in the intestine. It is very possible that the epithelial cells of the stomach become differentiated physiologically, and give rise to gastric juice, taking on the form of goblet-cells in the process. It cannot at present be stated whether the ciliated epithelial cells can absorb the food, or whether absorption is limited to non-ciliated cells lying amongst them. The lymphoid tissue is probably of great importance in the processes of assimilation (pp. 154–157, 159).

19. The branchial apparatus shows signs of considerable reduction.

Internal gills are present on the posterior surface of the hyoid, on both faces of the third and fourth branchial arches, and on the anterior face of the fifth. Three pairs of external gills were present on all specimens, even the largest, examined (pp. 161–163, and figs. 1, 17–19, and 70).

20. The pulmonary apparatus on the whole more nearly resembles the air-bladder and its duct of certain Ganoids than the lungs and laryngo-tracheal chamber of Amphibians. The view is expressed that the air-bladder of fishes and the lungs of higher Vertebrates are probably homologous structures. The pulmonary branches of the vagus cross one another at the base of the lungs, the left nerve supplying the right lung, and *vice versa* (pp. 163–167, and figs. 1, 21, 46, 47, and 71).

21. The blood is remarkable for the large size of its elements, and for the relatively large proportion of white corpuscles in comparison with red ones. Two kinds of the former are described, in one of which fine radiating pseudopodia can be protruded, and different stages in the degeneration of the nucleus and cell body could be observed (pp. 167–172, and figs. 48, and 64–66).

22. The chief points of special interest ascertained with regard to the blood-vessels are as follows (pp. 173–183, and figs. 18–22, 44–47):—

1. The presence of a paired pulmonary artery, the left supplying the ventral, and the right the dorsal, aspect of the lungs. Owing to the reduction of the branchial apparatus, their origin from the sixth primary aortic arch can no longer be made out.
2. The presence of a single true postcaval, along with a persistent left posterior cardinal.
3. The single caudal vein, giving rise to a right and a left renal portal.

23. No external sexual differences could be observed, and amongst the specimens examined, females were the more abundant (p. 114).

24. The urinogenital organs are surrounded by a quantity of tissue resembling the large celled lymphoid tissue of the gut, but differing from

the latter in becoming largely converted into adipose tissue (p. 184, and figs. 21, 49, 51, 53, 56–61).

25. The kidneys probably represent the mesonephros, and their duct the Wolffian duct. Nephrostomes are absent (pp. 186–188, 196, and figs. 21 and 56).

26. Comparatively small male specimens were in some cases found to be sexually mature. In unripe males, delicate Mullerian ducts are present. The sperm is conducted to the exterior by a duct which is probably formed in connection with the testis, quite independently of the excretory apparatus, and, therefore, to a certain extent comparable to that of Teleosts. The seminal tubules are directly connected with it, and it opens into the base of the Müllerian duct, the rest of which apparently aborts completely (pp. 188–191, and figs. 49-52, and 57-61).

27. Unlike most of the tissue elements, which are very large, and closely resemble those of the Amphibia, the spermatozoa are very minute, and in this respect differ markedly from the male sexual elements in this class. They are remarkable in possessing two free vibratile flagella attached to the carrot-shaped "head" (pp. 191, 192, and fig. 62).

28. The generative organs of the female bear a striking resemblance to those of Amphibians. The oviduct, doubtless, corresponds to the Müllerian duct: the lining epithelium shows in places signs of degeneration, and indications of a wandering of the blood-corpuscles into its lumen, such as has been observed in certain Urodeles, could be observed (pp. 192–194, and figs. 21 and 53).

29. No traces of a sympathetic were found (p. 110).

30. An account of the mode of life of Protopterus during the torpid period is given. The "cocoon" which is formed by the secretion from the integumentary glands impregnated with earthy salts, is provided with a "lid" perforated by a small aperture leading into a funnel-shaped tube, which passes between the lips of the animal, and thus forms a passage for the respiratory current. The presence of a gluey mucus between the body of the animal and the cocoon accounts for the persistence of the superficial sensory organs during the terrestrial life of the animal (pp. 201–205, and figs. 67–69).

31. The source of nutriment during the torpid period lies in the adipose tissue in connection with the gonads and kidneys and along either side of the notochord in the tail, as well as in the lateral muscles, some of which, especially in the caudal region, undergo a granular degeneration. Very possibly the latter is the precursor of the fatty degeneration, and in all probability leucocytes are the active transporting agents of the degenerated material. This assumption would help to explain the large development of lymphoid tissue in the body of the animal (pp. 206–211, and figs. 1, 22, 23, 24).

32. An analysis of the muscles shows that they do not retain quantities of the products of nitrogenous excretion, as is the case in Elasmobranchs (p. 212).

33. The structure of Protopterus is throughout compared, as far as is possible in the present state of our knowledge, with that of Lepidosiren and Ceratodus, as well as with other Ichthyopsida.

Various views have been expressed at different times as to the systematic position of the Dipnoi, some Zoologists placing them nearer the Elasmobranchii, or more especially the Holocephali, others considering that they are more closely related to the Ganoidei (particularly the bony Ganoids), while by others again, they are supposed to approach the Amphibia. To discuss all these views in detail would prolong this Paper to too great a length, and I will, therefore, refer the reader to the chief works on this subject quoted in the course of the present Memoir and in the Bibliography (p. 224). Having recorded my own observations on Protopterus, I must leave the question of generalization to future workers, as we have not at present, it seems to me, sufficient data to warrant any very definite conclusions being drawn as to the phylogeny of this interesting group.

We know from a study of Palæontology that Ceratodus has lived on from Devonian times, and that in the Palæozoic epoch a number of forms existed which were probably allied to the Dipnoi, but which were already highly specialized.* These facts at any rate show that the Dipnoi are the

* *Cf.* A. Smith Woodward (Catalogue of Fossil Fishes in the British Museum," vol. ii., 1891, Introduction).

representatives of a very ancient group. Of their ontogeny we know nothing, though it is probable that the ovum is invested with a gelatinous secretion from the walls of the oviduct, that it undergoes a complete and unequal segmentation, and that the young pass through a larval stage.

As it is impossible to decide how far the various resemblances in structure which exist between Dipnoans on the one hand, and certain Fishes and Amphibians on the other, indicate any real relationship, it is perhaps inadvisable to construct hypothetical genealogical trees indicating the possible phylogeny of the group, for, after all, these do not materially add to our knowledge, as they only represent the views of the observers who make them; and, from the nature of the case, these views are founded on insufficient data.

A glance through the abstract given above, as well as a study of the skeleton and nervous and muscular systems will, I think, show that although Protopterus has many points of resemblance to certain Elasmobranchs* and Ganoids on the one hand, and to the lower Amphibians on the other, it presents so many distinctive characters—some primitive and others specialized—that it must be placed at a great distance from either class, and the same may be said of Lepidosiren and Ceratodus (*cf.* 10). It is certainly inadvisable to retain the Dipnoi amongst the Fishes, as is still done by some Zoologists,† and it would be still more undesirable to place them with the Amphibia. The fact that they show a tendency towards a semi-terrestrial type as regards the respiratory organs and pelvis does not necessarily indicate any relationship to the Amphibia, any near connection with which

* The structure of Chlamydoselache (*vide* Garman, Bull. Mus. Comp. Zool., Harvard Coll., XII., No. 1, 1885) shows what widely divergent types of Elasmobranchs exist at the present day.

† In Hatchett Jackson's encyclopædic work (Rolleston's Forms of Animal Life) the Dipnoi are included under the Pisces. A reference to the characters of the class given on pp. 409–430 will, I think, show that this grouping was largely due to our imperfect knowledge of the Dipnoi, which, amongst other things, are said to be characterized by having no true glands in the integument, no iris, and no postcaval. I might here call attention to the fact that integumentary glands are present in some fishes, though their form and structure is very different from that seen in Protopterus and Amphibians. *Cf.* W. N. Parker "On the Poison-Organs of Trachinus," Proc. Zool. Soc., 1888; and A. Bottard, "Les Poissons Vénéneux," Paris, 1889.

is at once negatived by the structure of the paired fins, which show no tendency towards the evolution of a cheiropterygium. Even if we suppose with Beard * and others, that the lungs of the Dipnoi have an entirely different morphological significance from the air-bladder of Ganoidei and Teleostei (and this I cannot admit), there is no reason why the former should not have become independently developed in two groups standing widely apart from one another, if the necessity for such a respiratory apparatus should occur in both. And the same might be said with regard to the modifications of the heart, the presence of a postcaval, of multicellular integumentary glands, and so on. And on the other hand, the possession of cycloid scales, an ichthyopterygium, a spiral valve, and other piscine characteristics, does not prove near relationship to any particular group of living Fishes.

In a former Paper (22) I stated that "the facts I have mentioned are only some out of a great number which go to prove that a near connection must have existed between the ancestors of the Dipnoi and those of the Amphibia after they had diverged from a common piscine type, for the resemblances between the existing forms of both groups are exceedingly close. Nevertheless, certain points in the structure of the Dipnoi, more especially that of their fins, show that no direct relationship can exist between them and the Amphibia at the present day." I should now not be inclined to suppose that the connection between the Dipnoi and the Amphibia was even so close as this: all that can be said with anything like certainty until we know something of the development of the Dipnoi, is, that they are the isolated survivors of an exceedingly ancient group, which was probably nearly allied to the ancestors of existing Amphibians and Fishes—more particularly Elasmobranchs,† though the Ganoid stock most likely arose not far off.

Though retaining many primitive characters, the Dipnoi, and more particularly Protopterus and Lepidosiren, are in some respects highly

* *Loc. cit.*, on p. 167.

† Though in many points the Dipnoi certainly resembles Chimæroids more than other Elasmobranchs, it must not be forgotten that in others they more nearly approach the sharks—particularly that isolated and ancient form, Chlamydoselache. Possibly the recent discovery of

specialized, the specialization being largely due to a change of habit. The type of fin found in these two genera has probably arisen by degeneration, and does not represent a primitive icthyopterygium, but originated from a form which is most nearly retained at the present day by the Chimæroids. The single lung of Ceratodus also indicates a more primitive condition than the double lung of the other two genera, and may be compared with the air-bladder of bony Ganoids. These and other characters show that Ceratodus is the least specialized of the Dipnoi, and this is to be accounted for by the fact that it has not been obliged to adapt itself for a life on land to such an extent as the other two genera.

The supposition of Ayers (1) that there is no real generic or specific distinction between Protopterus and Lepidosiren has been shown to be erroneous by Baur and Schneider,* and is further supported by my own observations regarding the branchial apparatus of the former animal. It would be surprising if natural selection had not been the cause of some differences between these two forms, which are so widely separated geographically.

remains of fishes in the Lower Silurian may throw some light on this subject (*vide* note in "Nature," Feb. 5th, 1891; Chas. D. Walcott, Biol. Soc. of Washington, Feb., 1891).

* *Loc. cit.* (*vide* p. 117).

[*Note in Press.*]—Since the above was printed, an interesting paper by Burckhardt has come into my hands ("Das Centralnervensystem von *Protopterus annectens*," Berlin, 1892). Taking the Selachians as a starting point, he concludes that, although the brain of Protopterus is formed on a special type, it leans towards that of Amphibians, while that of Ceratodus is more reptilian.

LIST OF THE CHIEF PAPERS REFERRED TO TREATING SPECIALLY OF THE DIPNOI.

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(2.) BAUR, G.:
"Ueber *Lepidosiren paradoxa*," Zool. Jahrbücher, Bd. II., p. 575, 1887 (Bibliography given).

(3.) BEDDARD, F. E.:
"Observations on the Ovarian Ovum of Protopterus (Lepidosiren)," Proc. Zool. Soc. Lond., 1886; and "On the Development of the Ovum in the Dipnoi," Proc. Zool Soc. Lond., 1886.

(4.) BISCHOFF, Th.:
"*Lepidosiren paradoxa.*" Leipzig, 1840.

(5.) BOAS, E. V.:
"Ueber Herz und Arterienbogen bei Ceratodus u. Protopterus," Morph. Jahrb., Bd. VI., 1880.

(6.) GRAY, J. E.:
"Observations on a living African Lepidosiren in the Crystal Palace," accompanied by a note from Mr. A. D. BARTLETT, Proc. Zool. Soc. Lond., 1856, p. 342.

(7.) GÜNTHER, A.:
"Description of Ceratodus," Phil. Trans., vol. clxi., 1871.

(8.) HOWES, G. B.:
"On the Skeleton and Affinities of the Paired Fins of Ceratodus, with Observations upon those of the Elasmobranchii," Proc. Zool. Soc. Lond., 1887, p. 3.

(9.) HUMPHRY, G. M.:
"The Muscles of *Lepidosiren annectens*, with the Cranial Nerves," Journ. of Anat. and Physiol., vol. vi., 1872.

(10.) HUXLEY, T. H.:
"*Ceratodus fosteri*," Proc. Zool. Soc. Lond., 1876.

(11.) HUXLEY, T. H.:
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(12.) HYRTL, J.:
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(17.) LANKESTER, E. RAY:
"On the Hearts of Ceratodus, Protopterus, and Chimæra," Trans. Zool. Soc. Lond., vol. x., pt. II., 1879.

(18.) M'DONNELL, R.:
"Observations on the Habits and Anatomy of the *Lepidosiren annectens*," Roy. Dublin Soc. Journ. II., 1858–1859; and "Notiz über *Lepidosiren annectens*," Zeitschr. f. wiss. Zool., Bd. x., 1860.

(19.) NATTERER, J.:
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(20.) OWEN, R.:
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(21.) PARKER, W. N.:
"Zur Anat. u. Physiol. von *Protopterus annectens*," Berichte d. Naturforsch. Gesellschaft zu Freiburg, i/B, 4 Bd., 3 Heft, 1888. See also "Nature," vol. xxxix., p. 9, 1888; and Trans. Cardiff Naturalists' Soc., vol. xx., 1888.

(22.) PARKER, W. N. :

"On the Occasional Persistence of the Left Posterior Cardinal Vein of the Frog, with Remarks on the Homologies of the Veins of the Dipnoi," Proc. Zool. Soc. Lond., 1889.

(23.) PAULSON, O. :

"Die Epidermis von *Protopterus annectens*," Acad. Imp. d. Sciences de St. Petersbourg, Mélanges Biologiques, T. 4 (Aus dem Bulletin, T. 8, p. 141–145), 22 Sept. and 4 Oct., 1864.

(24.) PETERS, W. :

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(25.) STUHLMANN, F. :

"Zweiter Bericht über eine mit Unterstutzung d. Königl. Akad. d. Wissensch. nach Ost-Africa unternommene Reise. 3. Bemerk. über die Süsswasserfauna von Quellimane." Sitzungsber. d. Königl. preuss. Akad. d. Wissenschaften zu Berlin, 32, 1889.

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(29.) WIEDERSHEIM, R. :

"Das Skelet- u. Nervensystem von *Lepidosiren annectens*" (*Protopterus*), Morphol. Studien, Heft I. Jena, 1880.

(30.) WIEDERSHEIM, R. :

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LIST OF ABBREVIATIONS USED IN THE FIGURES ON PLATES VII. TO XVII.

a. d. . . . Adipose tissue.
af. br. . . . Afferent vessels of the internal gills, or of corresponding arches : [1] of hyoid ; [2–6] of branchial arches.
af. e. br. . . Afferent vessels of external gills.
al. s. . . . Alisphenoid cartilage.
a. n. . . . Anterior nostril.
ang. . . . Angulare.
ans. . . . Anastomoses between post-caval and left cardinal vein.
a. o. . . . Dorsal aorta.
ao. r. . . . Roots of aorta.
a. p. . . . Abdominal pore.
a. t. . . . Atrium.
au. . . . . Auditory capsule.

b. . . . . Bony tissue of teeth.
b. c. . . . Basis cranii.
b. d. . . . Common bile-duct.
b. d.[1] . . . Aperture of bile-duct.
b. ent. . . . Bursa entiana.
bl. c. . . . Blood corpuscles.
bl. v. . . . Blood-vessel.
b. m. . . . Basement membrane.
br. n. . . . Brachial nerve.
b. o. . . . Basi-occipital.
br. . . . Gills.
br. a.[1–5] . . Branchial arches.
br. c. . . . Branchial chamber.
br. cl.[1–4] . . Branchial clefts.
br. plx. . . Brachial plexus.
b. st. . . . Branchiostegal rays.

c. a. . . . Conus anteriosus.
c. ao. . . . Caudal aorta.
car. . . . Carotid artery.
cb. . . . . Cerebellum.
cd. v. . . . Left cardinal vein.
cœ. . . . . Cœlome.
c. f. . . . Caudal fin.
c. h. . . . Prosencephalon.
cl. . . . . Cloaca.
cl. c. . . . Cloacal cæcum.
c. m. a. . . Cœliaco-mesenteric artery.
c. msc. . . . Circular muscles.
coc. . . . . Cocoon.
com. . . . Posterior commissure.
cn. f. . . . Connective-tissue fibres.
cr. . . . . Cranial rib and its muscles.
cr. a. . . . Artery to muscles of cranial rib.
cut. . . . Cuticular border of epidermis.
c. v. . . . Caudal vein.
cy. a. . . . Cystic artery.
cy. d. . . . Cystic duct.

d. . . . . Duct.
der. . . . . Derma.
d. f. . . . Dorsal fin.

d. m. . . . Dorsal mesentery.
dn. . . . Dentary.
dn. c. . . . Coronoid process of dentary.
dnt. . . . Dentine.

earth. . . . Earthy mass round cocoon.
earth. t. . . Burrow through earthy mass round cocoon.
e. . . . . . Eye.
ef. br. . . . Efferent vessels of internal gills or corresponding arches : [1] of hyoid; [2-6] of branchial arches.
ef. e. br. . . Efferent vessels of external gills.
e. m. . . . Eye-muscles.
en. . . . . Enamel epithelium.
ep. . . . . Epithelium.
ep. f. . . . Epithelial folds.

f. . . . . Adipose tissue.
f. b. . . . Longitudinal band of fibres and fatty tissue.
f. p. . . . Fronto-parietal.
f. r. . . . Cartilaginous fin-rays.
f. t. . . . Fibrous tissue.

g. a. . . . Gastric artery.
g. b. . . . Gall-bladder.
g. c. . . . Goblet-cells.
g. c.[1] . . . Aperture of goblet-cell.
gld. . . . Multicellular gland of integument.
gld.[1] . . . Aperture or duct of integumentary gland.
glom. . . . Glomerulus.
g. p. . . . Genital papilla.
gr. . . . . Granules in degenerating muscle fibres.
gr. c. . . . Granular cells of lymphoid-tissue ("wander-cells").
g. v. . . . Gastric vein.

h. . . . . Horny cap of teeth.
h. a. . . . Hæmal arch.
h. b. . . . Hyoid hemibranch.
h. d. . . . Hepatic duct.
hp. a. . . . Hepatic artery.
hp. v. . . . Hepatic portal veins.
h. r. . . . Horny rays of fin.
h. sp. . . . Hæmal spine.
ht. . . . . Heart.
ht. c. . . . Cartilage of septum of heart.
h. v. . . . Hepatic veins.
hy. . . . . Hyoid cartilage or bone.
hy. br. . . . Hyobranchial cleft.

i. c. a. . . . Intercostal arteries.
i. c. v. . . . Intercostal veins.
i. int. v. . . Intra-intestinal vein.
i. j. . . . . Inferior jugular vein.
int. . . . . Intestine.
ir. . . . . Iris.
i. sp. . . . Interspinous bones.

j. . . . . Jugular (anterior cardinal) vein.

k. . . . . Kidney.
k. d. . . . Duct of kidney.
k. d.[1] . . . Aperture of duct of kidney in urinogenital sinus or cloaca.

l. . . . . Lips.
l. c. . . . Labial cartilage.
ld. . . . . "Lid" of cocoon.
ld. p. . . . "Pipe" from lid of cocoon.
ld. p.[1] . . . Aperture leading into "pipe."
leu. . . . . Leucocytes.
lg. . . . . Lung ([1] right, [2] left lung).
l. l. . . . . Lateral line.
l. m. . . . Lateral muscles.
l. msc. . . . Longitudinal muscles.
lr. . . . . Liver.

ls. . . . . Lens.
ly. . . . . Lymphoid tissue.
ly. ad. . . . Lympho-adenoid tissue (corpora adiposa).
ly. ep. . . . Subepithelial lymphoid tissue.
ly. f. . . . Small-celled lymphoid tissue ("lymphoid follicles").
ly. n. . . . "Nests" of lymphoid tissue beneath epidermis.

m. . . . . Mouth.
m. a. [1, 2, 3, v] . Mesenteric arteries.
m. b. . . . Mesencephalon.
m. c. . . . Muscular coat.
mck. . . . Meckel's cartilage.
m. d. . . . Müllerian duct.
m. d.[1] . . . Abdominal aperture of Müllerian duct.
m. f. . . . Folds of mucous membrane.
m. m. . . . Muscularis mucosæ.
mn. . . . Mandible.
mn. t. [1, 2, 3] . Mandibular teeth.
m. o. . . . Myelencephalon.
msc. . . . Longitudinal or scattered muscular bands of spiral valve.
mso. . . . Mesorchium.
m. v. . . . Mesenteric vein.

n. . . . Nerve.
n. a. . . . Neural arch.
na. c. . . . Nasal cartilage.
nc. . . . . Notochord.
n. sp. . . . Neural spines.
nu. . . . . Nucleus.

od. . . . . Odontoblasts.
œs. . . . . Œsophagus.
œs. v. . . . Œsophageal veins.
ol. . . . . Olfactory organ.
ol. l. . . . Rhinencephalon.
op. . . . . Opercular bone.
op. l. . . . Optic lobe.
o. pr. s. . . Orbito-presphenoid cartilage.
op. th. . . . Optic thalamus.
ov. . . . . Ovary.
ovd. . . . . Oviduct.
ovd.[1] . . . Abdominal aperture of oviduct.
ov. v. . . . Ovarian veins.

p. a. . . . Pulmonary artery ([1] left, or ventral; [2] right, or dorsal).
pa. ch. . . . Parachordal cartilage.
pan. . . . Pancreas.
pan. a. . . . Pancreatic artery.
pan. d. . . . Pancreatic duct or ducts.
pan. t. . . . Pancreatic tubules.
pa. s. . . . Parasphenoid.
pa. v. . . . Veins from body-walls.
pc. a. . . . Pectoral arch.
pc. l. . . . Pectoral fin.
per. . . . Pericardium.
pg. . . . . Pigment cells([1] yellow, [2] brown, [3] black).
pit. . . . . Pituitary body.
pl. . . . . Pelvis.
pl. a. . . . Pelvic artery.
pl. l. . . . Pelvic fin.
pl. v. . . . Pelvic vein.
plt. . . . . Palatine artery.
p. n. . . . Posterior nostril.
p. pg. . . . Palato-pterygoid or palato-quadrate.
p. pg. t.[1, 2] . Palato-pterygoid teeth.
pr. c. . . . Precaval (Cuvierian) vein.
pr. o. . . . Pro-otic cartilage.
pt. . . . . Peritoneum.
pt. c. . . . Postcaval.
p. v. . . . Pulmonary vein.
py. v. . . . Pyloric valve.

q. . . . . Quadrate.

r. . . . . Rib.
r. a. . . . Renal arteries.
rc. . . . . Rectum.
r. p. . . . Renal portal vein.
r. v. . . . Revehent renal veins.
rt. . . . . Retina.
rt. ao. . . . Root of aorta.

sa. . . . . Sarcolemma.
sc. . . . . Scales.
s. cl. a. . . Subclavian artery.
s. cl. v. . . . Subclavian vein.
s. eth. . . . Supra-ethmoid.
s. mx. . . . Submaxillary artery.
s. n. . . . Septum nasi, or nasal roof.

sn. o. . . . Sensory organs of integument.
sn. o.[1] . . . Taste-bud.
sn. t. . . . Sensory tube.
s. o. . . . Supra-occipital.
s. orb. . . . Supra-orbital.
sp. . . . . Spleen.
sp. c. . . . Myelon.
sp. d. . . . Sperm-duct.
sp. d.[1] . . . Sperm-duct after uniting with base of Müllerian duct.
spl. . . . . Splenial.
sp. n. . . . Spinal nerve.
sp. v. . . . Spiral valve.
sq. . . . . Squamosal (pre-operculum).
st. . . . . Stomach.
str. . . . . Striated border of epithelium.

t. . . . . Tongue.
th. . . . . Thyroid.
tl. . . . . Tail.
tm. . . . . Thymus.
t. msc. . . . Muscles of tongue.
t. p. . . . Papillæ of tongue.
tr. . . . . Trabecular or parachordal cartilages.
tr. p. . . . Transverse process.
ts. . . . . Testis.
ts. l. . . . Lobes or lobules of testis.
ts. t. . . . Tubules of testis.
ts. v. . . . Testicular veins.

u. g. p. . . Urinogenital papilla.
u. g. s. . . Urinogenital sinus.

v. . . . . Vent.
v. a. . . . Vertebral artery.
vb. . . . . Vestibule of lungs.
v. int. v. . . Ventral intestinal vein.
v. m. . . . Ventral mesentery.
vn. . . . Ventricle of heart.
v. t. . . . Vomerine teeth.
v. v. . . . Vertebral vein.

v. . . . . Trigeminal nerve.
x. . . . . Vagus nerve.
x. *b.* . . . Brachial branch of vagus.
x. *br.* . . . Branchial branch of vagus.
x. *ch.* . . . Chiasma of vagus.
x. *lat.* . . . Lateral branch of vagus.
x. *pul.* . . . Pulmonary branch of vagus.
xii. . . . . Hypoglossal.

The sections were drawn with the aid of an Oberhäuser camera lucida.

For figs. 1, 8–14, 25–28, 46, and 47, I am indebted to the artistic skill of Mr. T. H. Thomas, R.C.A., and I have to thank my friend Mr. L. B. Carslake for the original drawings of figs. 48–51, 53, and 67–69.

PLATE VII.

EXPLANATION OF PLATE VII.

Figure

1. Dissection of a female specimen from the left side, showing the viscera *in situ*. The left kidney, ovary, and oviduct have been removed. The numbered lines roughly correspond to the regions in which the transverse sections figured on Pls. VIII.–X., figs. 8–22, were taken. × 1½.

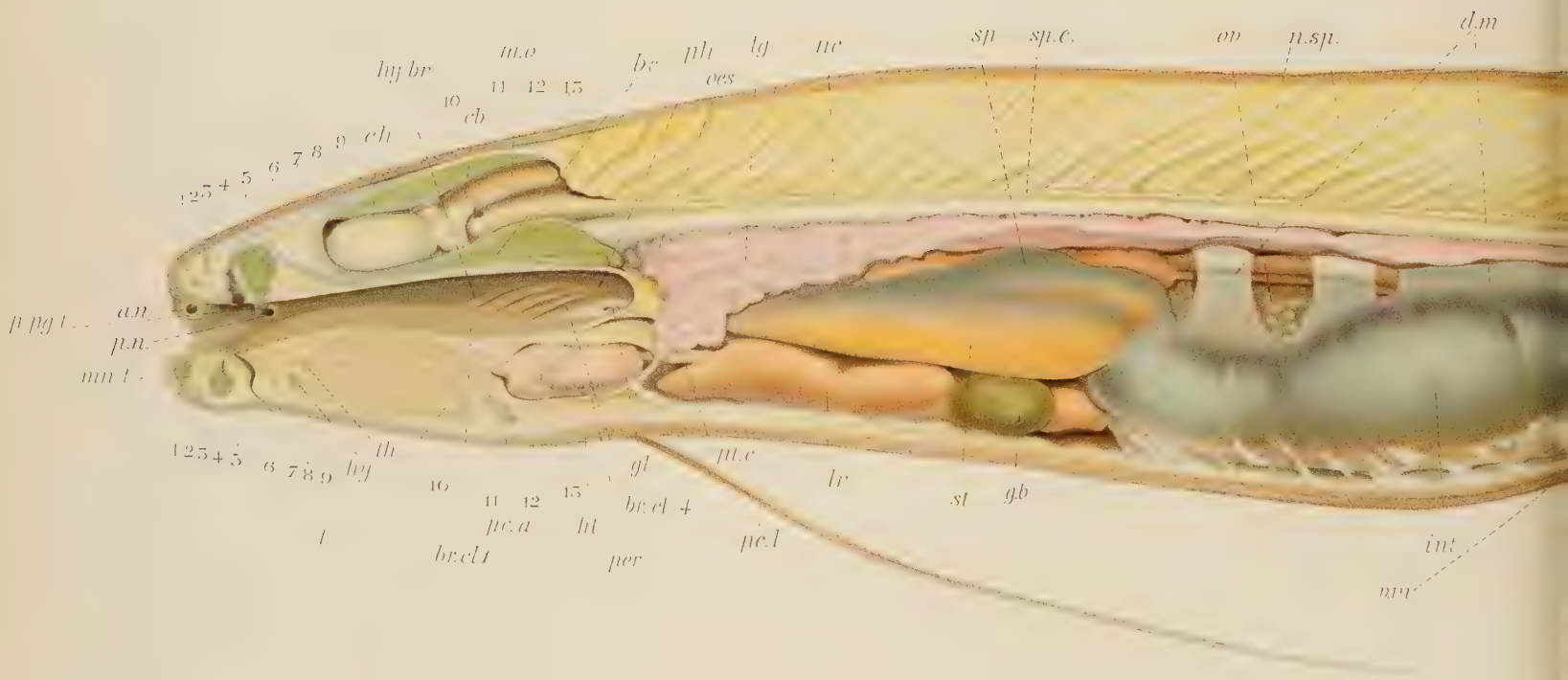
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PLATE VIII.

EXPLANATION OF PLATE VIII.

Figure

2. Transverse section through the integument of a young specimen (8 cm. in length) in the region of the snout. The section passes through a multicellular gland. Chromic acid and borax carmine.

3. Transverse section through a papilla of the tongue of a middle-sized specimen, showing a taste-bud at its apex. Chromic acid and borax carmine.

4. Semi-diagrammatic transverse section through the mandibular tooth of a small specimen (the enamel is not shown). Chromic and nitric acids, and borax carmine.

5. A–D. Epithelial cells from various regions of the intestine. Müller's fluid and carmine.

6. Transverse section through a part of the large-celled lymphoid-tissue of the intestine, from a specimen 8 cm. in length. Chromic acid and borax carmine.

7. Transverse section through the small-celled lymphoid tissue ("lymphoid follicle") of the intestine. From the same preparation as fig. 6.

Figs. 8–22 represent transverse sections of a young female, about 8 cm. in length and 1 cm. in dorso-ventral diameter. Chromic and nitric acids, and borax carmine. The numbers given below refer to the order of the sections in the complete series.

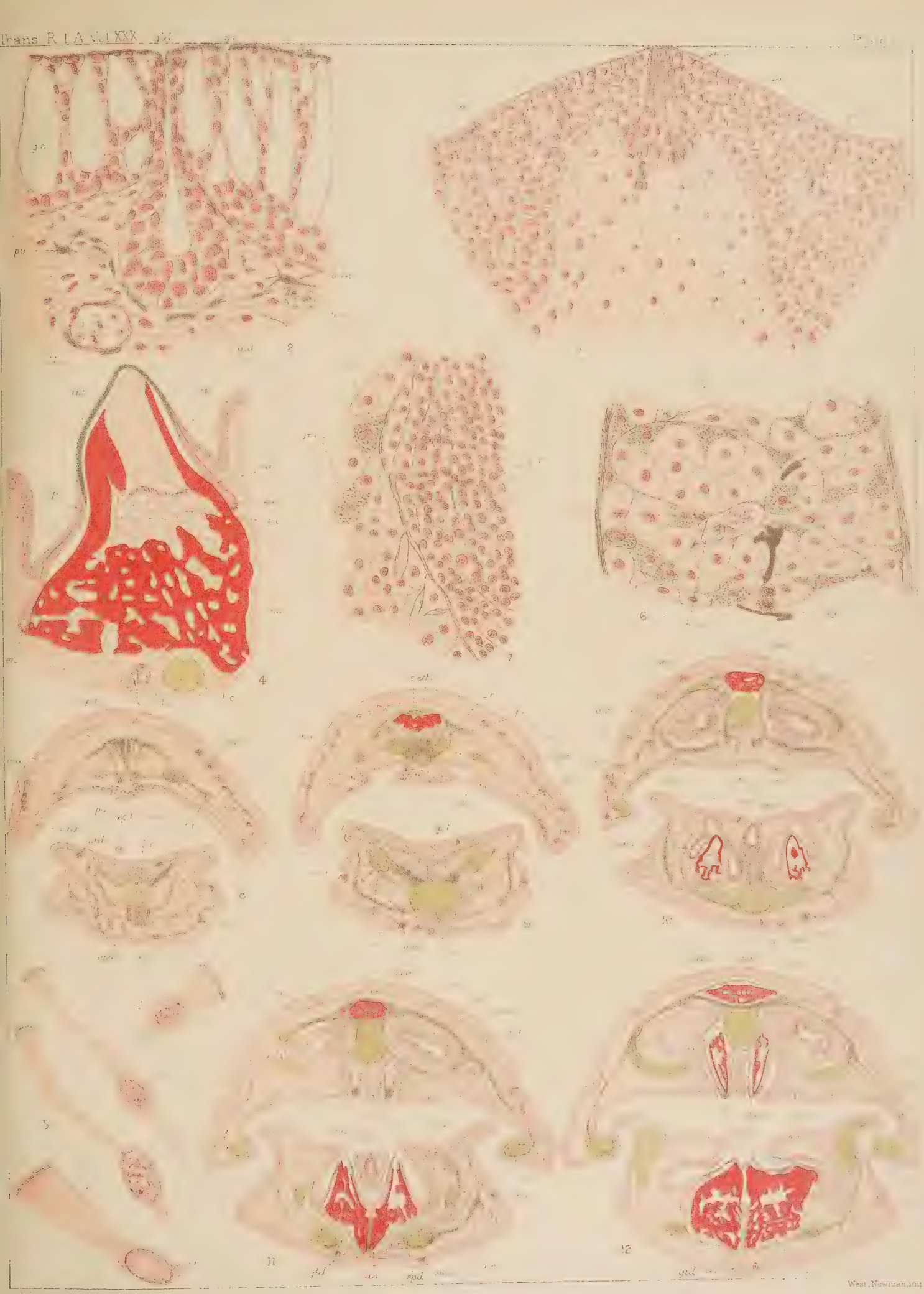
8. Section 48 (through line 1, in Pl. VII., fig. 1), anterior part of snout, in front of anterior nostrils.

9. Section 64 (through 2 in fig 1). Through the anterior nostril.

10. Section 87 (through 3 in fig. 1). Just behind the anterior nostril.

11. Section 97 (through 4 in fig. 1). Through the vomerine, and anterior points of the mandibular teeth.

12. Section 120 (through 5 in fig. 1). Through the anterior points of the palatopterygoid teeth.



M.P.Parker chromo lith
West, Newman, imp.

PLATE IX.

EXPLANATION OF PLATE IX.

Figure

13. Section 155 (through 6 in fig. 1). Through the posterior nostrils and the anterior part of the tongue.

14. Section 227 (through 7 in fig. 1). Through the olfactory lobes, eyes, anterior part of the tongue, and hyoid.

15. Section 248 (through 8 in fig. 1). Through the anterior part of the prosencephalon, middle region of the tongue, and thyroid.

16. Section 278 (through 9 in fig. 1). Through the prosencephalon, tongue, lateral parts of the thyroid, and quadrate.

17. Section 374 (through 10 in fig. 1). Through the thalamencephalon and hyobranchial cleft.

18. Section 427 (through 11 in fig. 1). Through the mid- and hind-brain, pituitary body, anterior part of the branchial region, and conus arteriosus.

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West, Newman, lith.

EXPLANATION OF PLATE X.

Figure

19. Section 490 (through 12 in fig. 1). Through the myelencephalon, auditory capsules, branchial arches, and posterior part of the conus arteriosus.

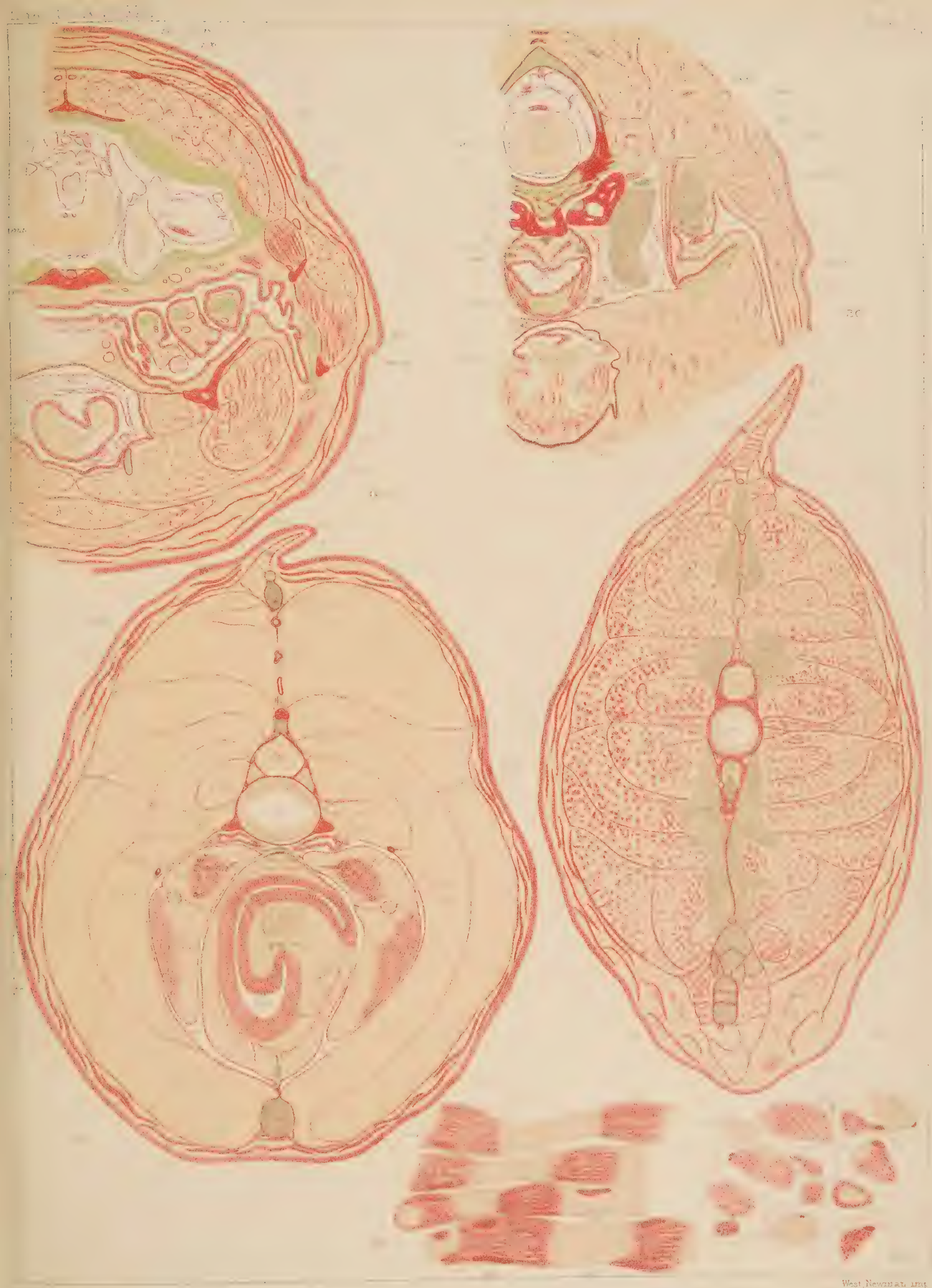
20. Section 550 (through 13 in fig. 1). Through the junction of the myelencephalon and myelon, the pharynx just anterior to the glottis, the thymus, and heart.

21. Section 1692 (through 14 in fig. 1). Through the body, a short distance posterior to the middle, showing intestine, ovaries, kidneys, lungs, &c.

22. Section 2232 (through 15 in fig. 1). Taken a short distance posterior to the cloaca, showing the caudal vessels, and adipose tissue amongst the lateral muscles.

23. Fibres from the lateral muscles of the tail, showing granular degeneration. Longitudinal section. Absolute alcohol and borax carmine.

24. The same as fig. 23, in transverse section.



West, Newman, imp.

PLATE XI.

EXPLANATION OF PLATE XI.

Figure

25. View of palate. The ventral wall of the right olfactory sac has been cut away so as to show the folds of the olfactory mucous membrane. × 4.

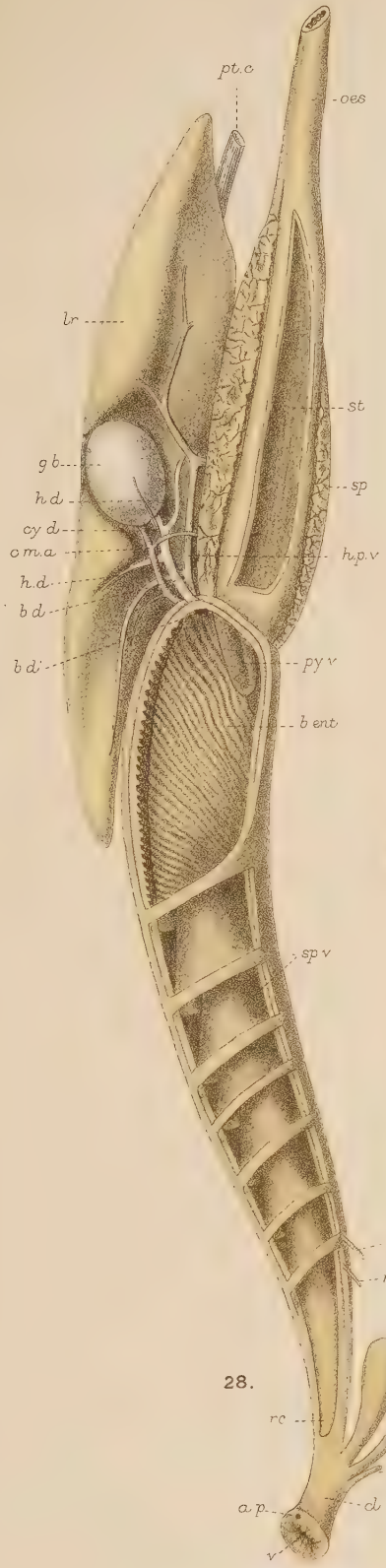
26. Left olfactory sac, the outer wall of which has been removed. × 4.

27. View of floor of mouth. The mucous membrane covering the posterior part of the tongue has been dissected away so as to show the thyroid. × 4.

27A. Transverse section through the thyroid. Chromic acid and borax carmine.

28. The alimentary canal of a female specimen, from the œsophagus to the vent, together with the liver, from the left side. Part of the left wall of the stomach and intestine has been cut away, and the peritoneal covering of the spleen removed. × 1½.

29. Dissection of the stomach, liver, spleen, and bursa entiana from the right side, to show the relations of the pancreas. The liver is displaced, the posterior part of the spleen (which is partly imbedded in the anterior end of the pancreas) cut away, and the peritoneum of the intestine dissected off. The position and relations of the bile and pancreatic ducts, as well as the extension of the pancreas towards the left side of the stomach and bursa entiana, are indicated by dotted lines. × 1¼.



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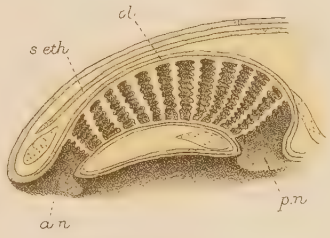

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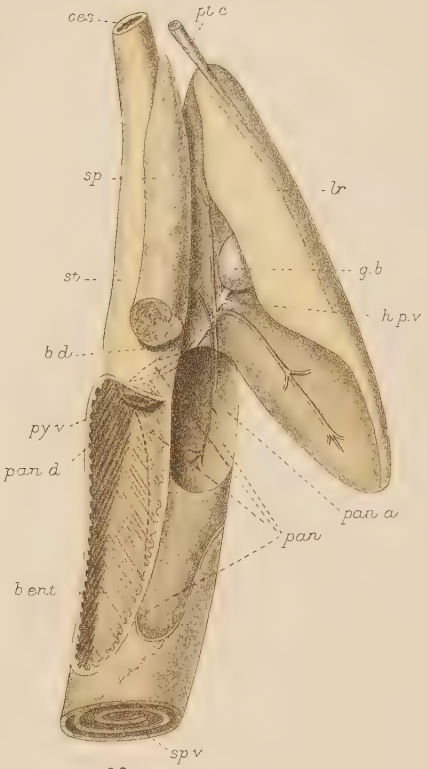

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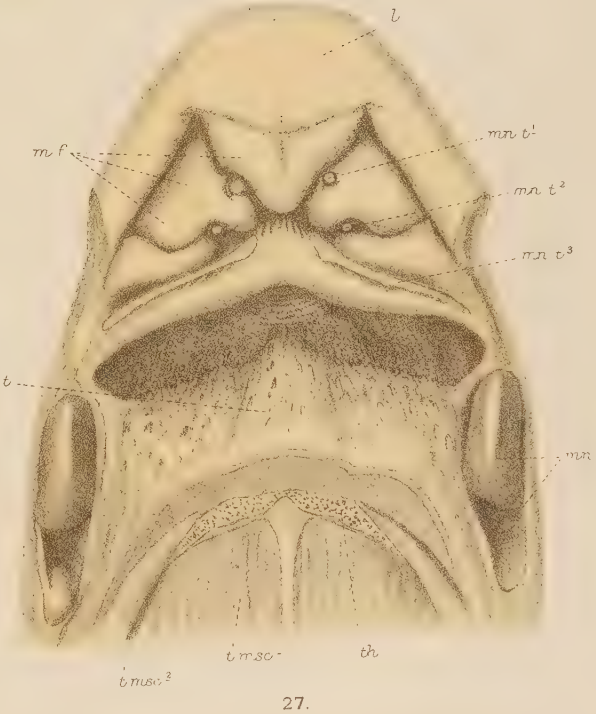

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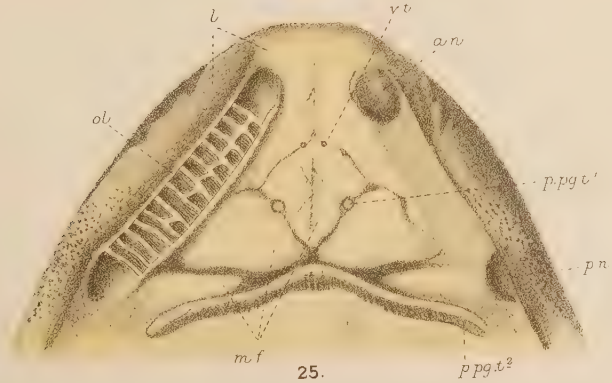


25.

27A.

W.N.P. & T.H.T. del. ad. nat.
M.P. Parker chromo. lith.
West, Newman, imp.

PLATE XII.

EXPLANATION OF PLATE XII.

Figure

30. Transverse section through the stomach and spleen, taken at about the middle of the former. Aceto-osmio-chromic acid, stained with picric acid and alum carmine.

31. Transverse section through the posterior part of the stomach and spleen, and anterior part of the pancreas, close to the junction of the bile and pancreatic ducts. Chromic acid and borax carmine.

32. Transverse section through the bursa entiana, pancreas, and anterior end of spiral valve. Aceto-osmio-chromic acid, stained with picric acid and alum carmine.

33. Transverse section through the intestine, taken at about the middle of its length. Preparation as in fig. 32.

34. Longitudinal section of the intestine from axis to periphery, taken at about the middle of its length. Preparation as in fig. 32.

35. Transverse section through the apex of one of the longitudinal folds of the oviducal mucous membrane. Corrosive sublimate, stained with picric acid and alum carmine.

W. N. Parker, del. ad. nat.
M. P. Parker chromo lith.
West, Newman, imp

PLATE XIII.

EXPLANATION OF PLATE XIII.

Figure

36. Surface view of a piece of the epidermis, to show the relation of the goblet-cells and their apertures to the rest of the epidermis. Stained with hæmatoxylin.

37. Transverse section through the integument of a middle-sized specimen just behind the gape, including a sensory tube lying beneath the general level of the epidermis. Chromo-osmio-ascetic acid and hæmatoxylin.

38. Transverse section of the integument from the posterior part of the body, passing through a sensory organ of the lateral line. Corrosive sublimate, stained with picric acid and alum carmine.

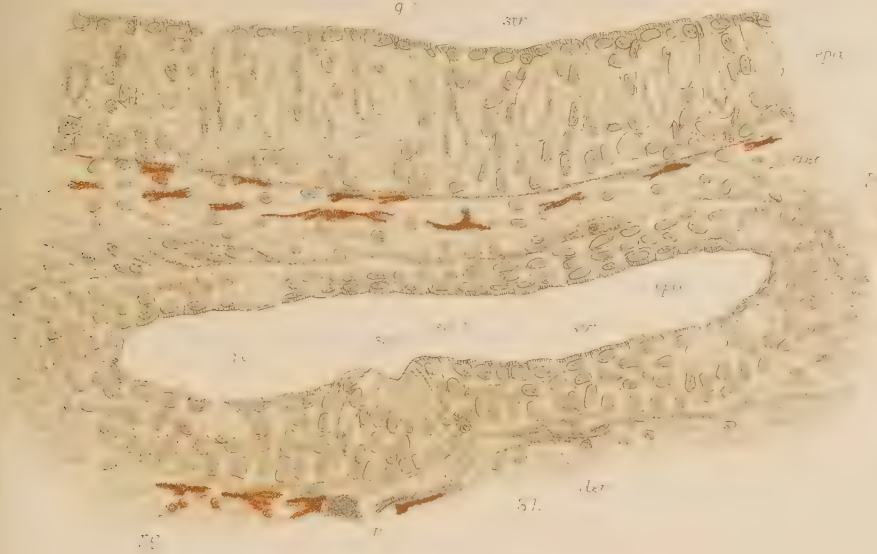
39. Transverse section through the epithelium of the posterior end of the stomach. Preparation as in fig. 38.

40. Longitudinal section through the spleen, towards its posterior end. Preparation as in fig. 38.

41. Transverse section through the pancreas ; A, through one of its ducts. Preparation as in fig. 38.

42. Transverse section through the lower part of one of the folds of mucous membrane of the bursa entiana. Preparation as in fig. 38.

43. Transverse section through the epithelium and lymphoid tissue of the spiral valve. Preparation as in fig. 38.



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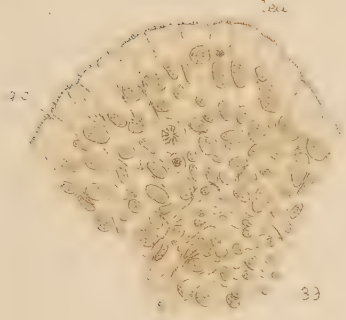

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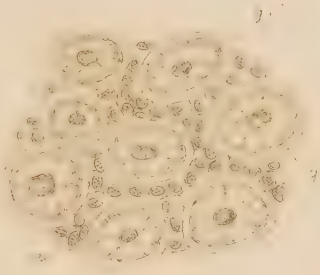

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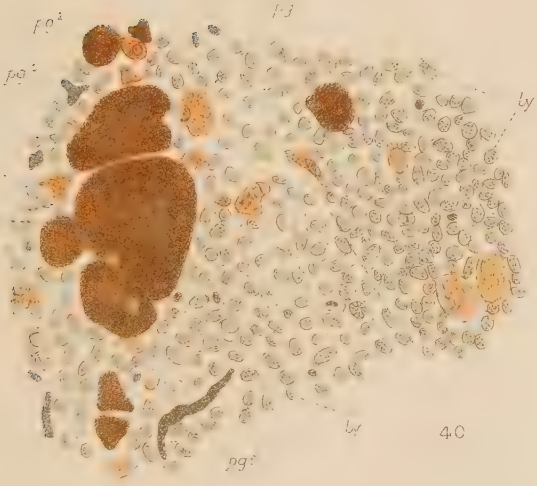

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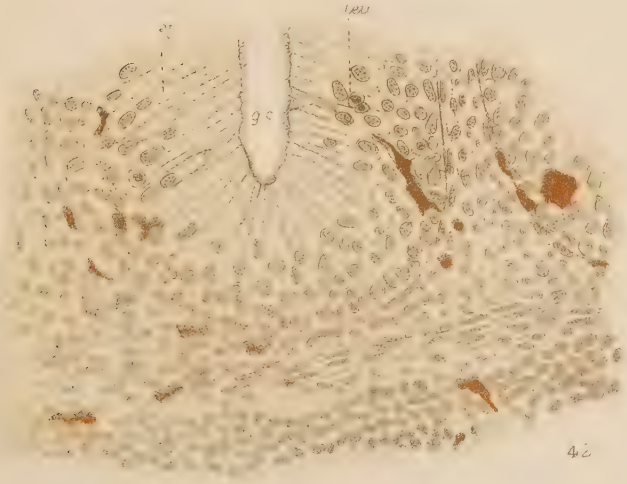

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West, Newman, imp

PLATE XIV.

EXPLANATION OF PLATE XIV.

Figure

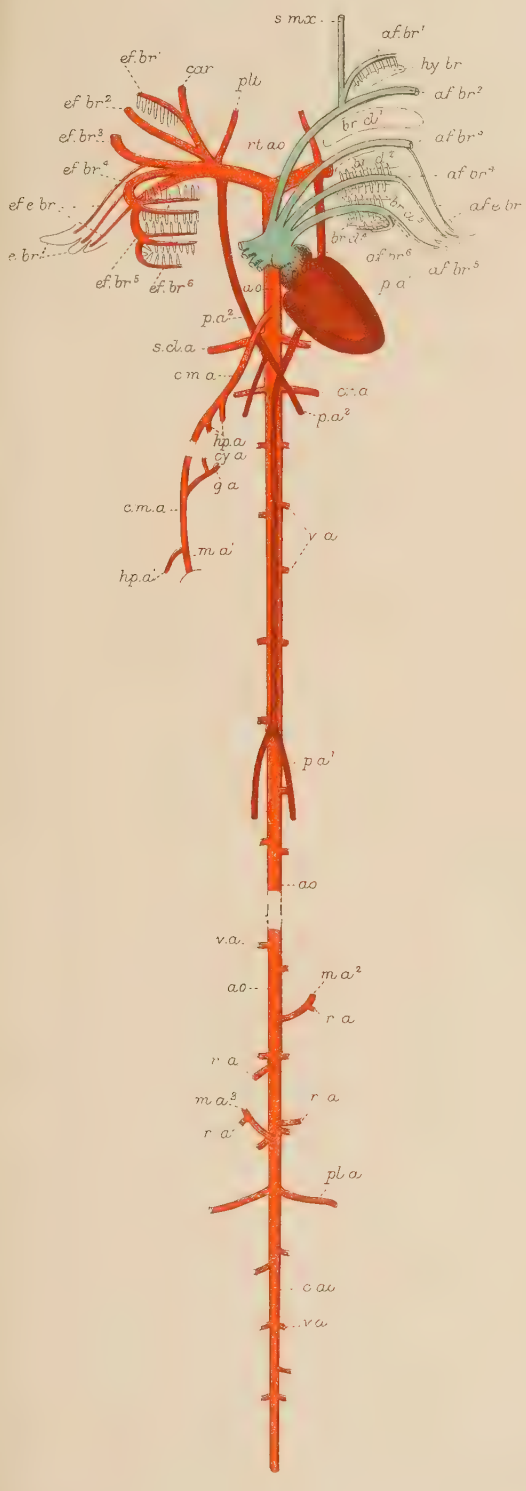
44. Diagram of the branchial vessels and chief arteries of the body, from the ventral side. Only the anterior and posterior ends of the abdominal portion of the aorta are shown.

45. Diagram of the chief veins. (For the pulmonary vein see fig. 46.)

46. The lungs and their vessels, from the ventral side. Part of the ventral wall of the pharynx and anterior end of the lungs has been removed. × 1½.

47. Anterior part of the lungs from the dorsal side, to show the relations of the dorsal pulmonary arteries and pulmonary nerves. The pharynx has been slit open dorsally. × 1½.

48. Blood corpuscles, treated by Ehrlich's method. A, colourless corpuscles of Form A; B, colourless corpuscles of Form B; C, red corpuscles.



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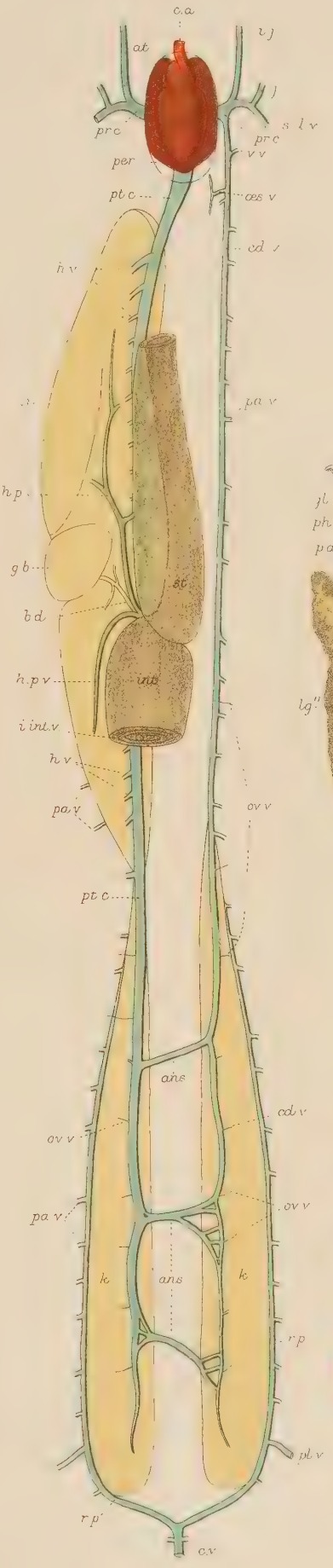

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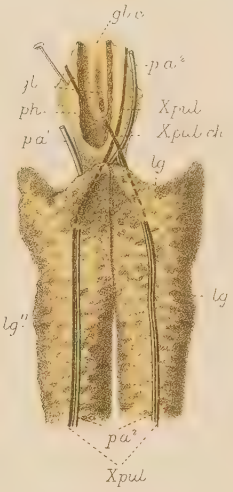

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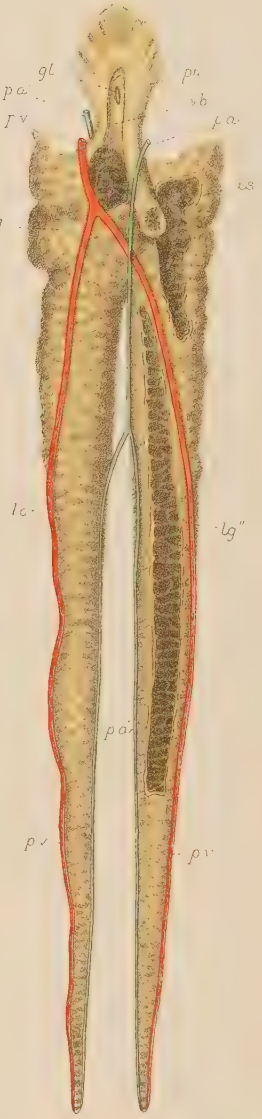

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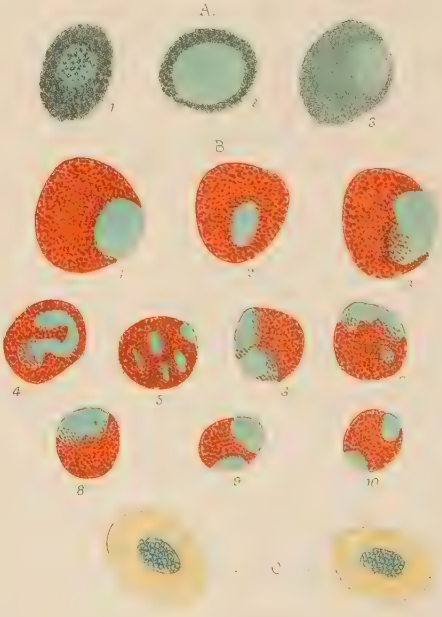


48.

W.N.P.T.H.T.& L.B.C. del ad nat.
M.P.Parker chromo.lith.

West, Newman. imp

PLATE XV.

EXPLANATION OF PLATE XV.

Figure

49. Urinogenital organs of a ripe male, from the ventral side. The peritoneum has been removed from the right side, and the cloaca slit open. × 1½.

50. Enlarged view of cloaca of same, to show the mode of termination of the urinary and genital ducts.

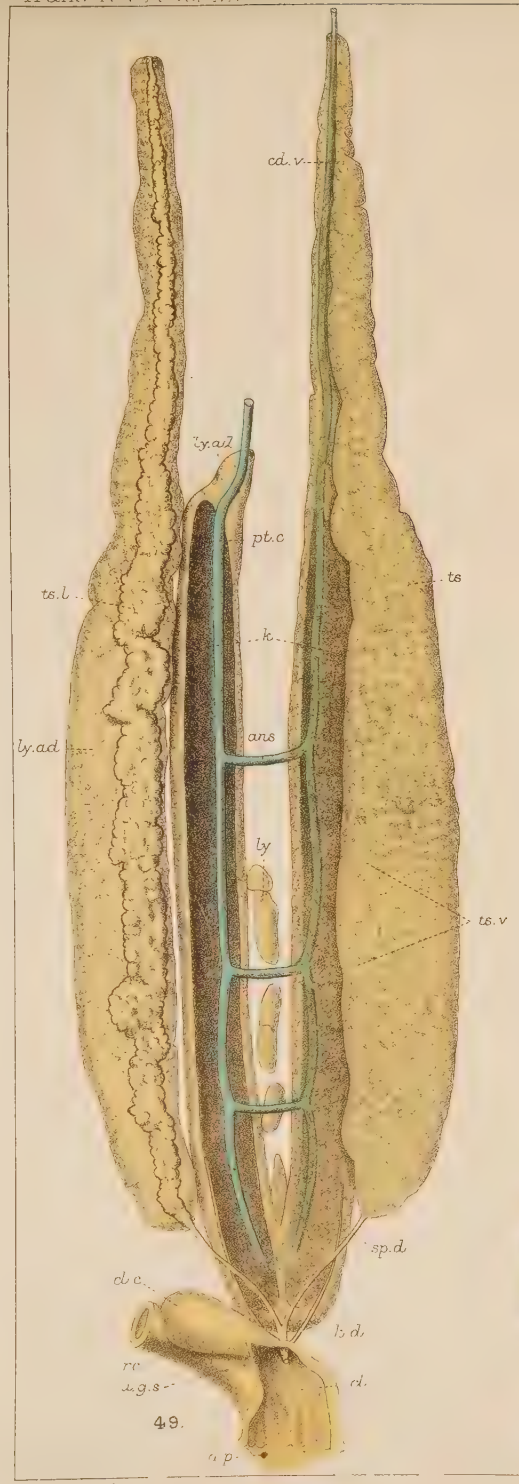
51. Urinogenital organs of the right side of an unripe male, from the dorsal side. The testis has been dissected away from the kidney so as to show the whole course of the vestigial Müllerian duct. × 1½.

52. Three transverse sections of the generative duct of the same specimen, taken in consecutive order (A, B, C), from before backwards, to show the junction of the sperm duct with the Müllerian duct.

53. Urinogenital organs of a ripe female, from the ventral side. The peritoneum has been removed on the left side. × 1½.

54. Part of section 2140 of the series described in reference with figs. 8–22, passing through the kidneys and their ducts, the fused portion of the oviducts, the cloacal cæcum, and the rectum.

55. Transverse section through part of the walls of the oviduct.



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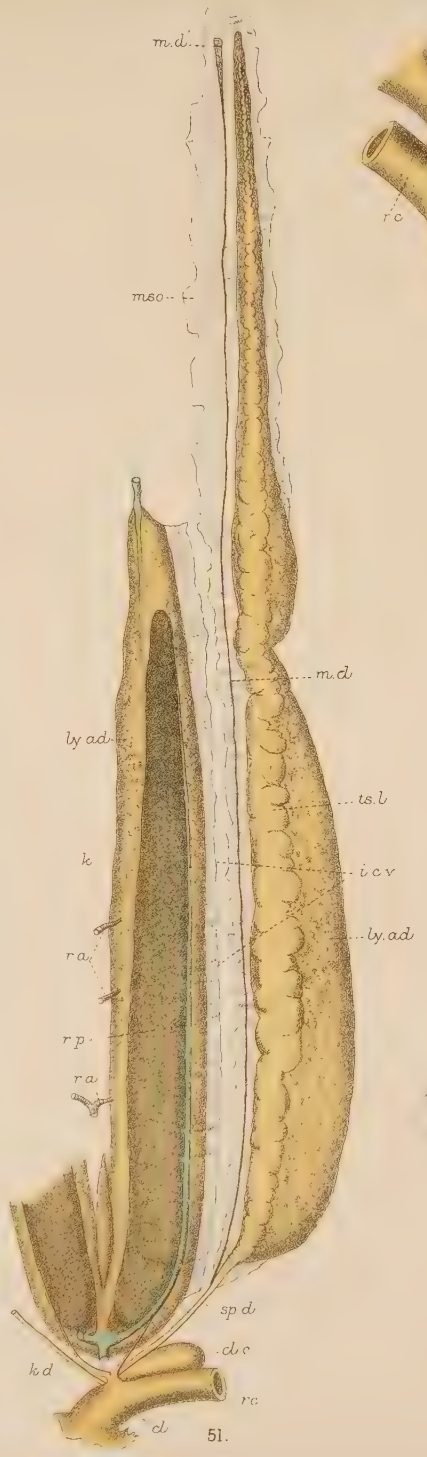

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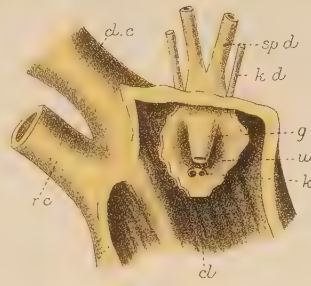

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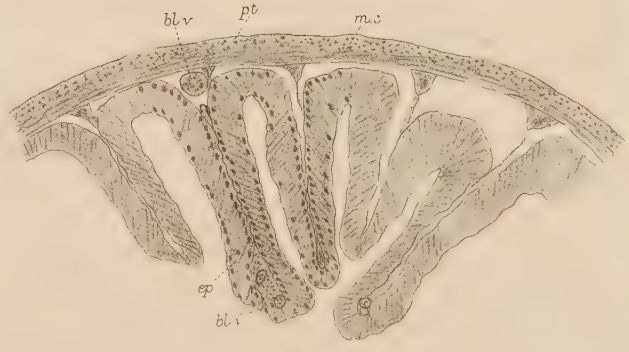

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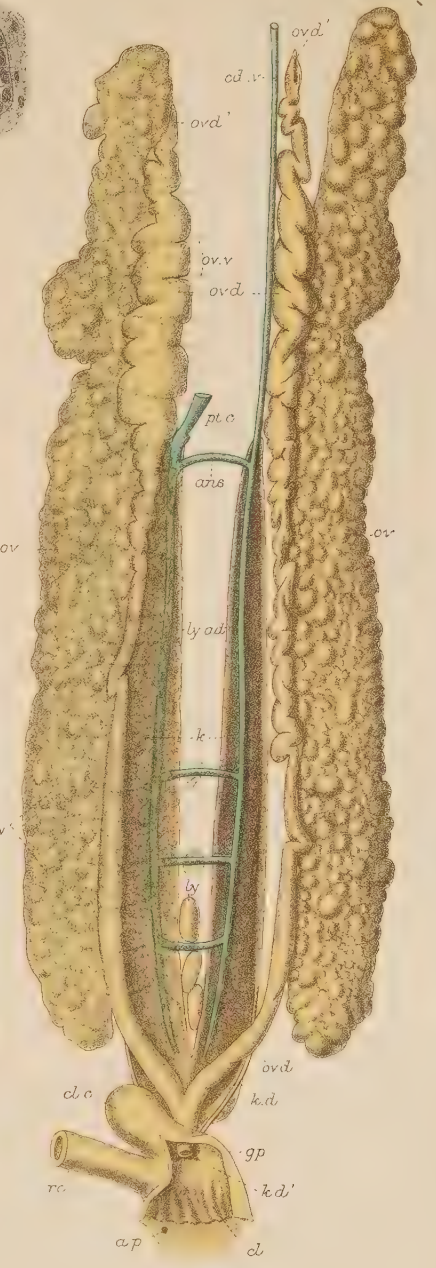


53.

W.N.P. & L.B.C. del. ad nat.
M.P. Parker chrom. lith.

West, Newman, imp

PLATE XVI.

EXPLANATION OF PLATE XVI.

Figure

56. Transverse section through the kidney of a male, at about the middle of its length. Chromic acid and borax carmine.

57. Transverse section through a ripe testis at about the middle of its length. Aceto-osmio-chromic acid and borax carmine.

58. Longitudinal section of same, slightly posterior to the middle of its length. Stained with hæmatoxylin.

59. Transverse section through the anterior narrower part of same. Preparation as in fig. 57.

60. Transverse section through the anterior narrower part of the testis of an unripe individual (see Pl. xv., fig. 51), showing the Müllerian duct. Müller's fluid and hæmatoxylin.

61. The same, but more anterior, so as to pass through the abdominal aperture of the Müllerian duct.

62. Spermatozoa—fresh, in salt solution.

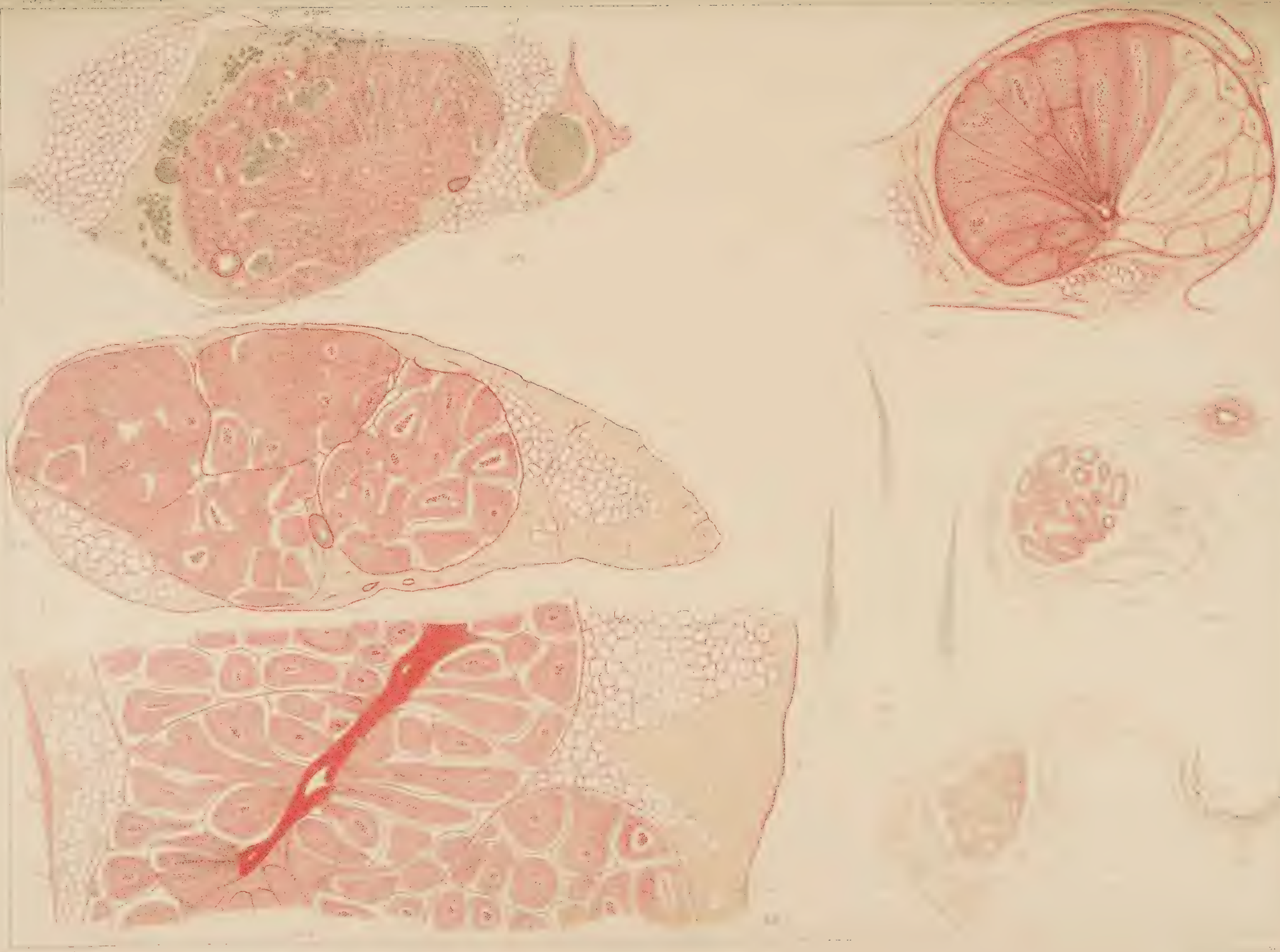


PLATE XVII.

EXPLANATION OF PLATE XVII.

Figure

63, A–F. Epithelial cells from various regions of the gut. Fresh, in salt solution.

64, A–C. Red blood-corpuscles. Fresh, in salt solution.

65, A–H. Colourless corpuscles of Form A. Fresh, in salt solution.

66, A–I. Colourless corpuscles of Form B. Fresh, in salt solution.

(Figs, 64, 65, and 66, are drawn to the same scale.)

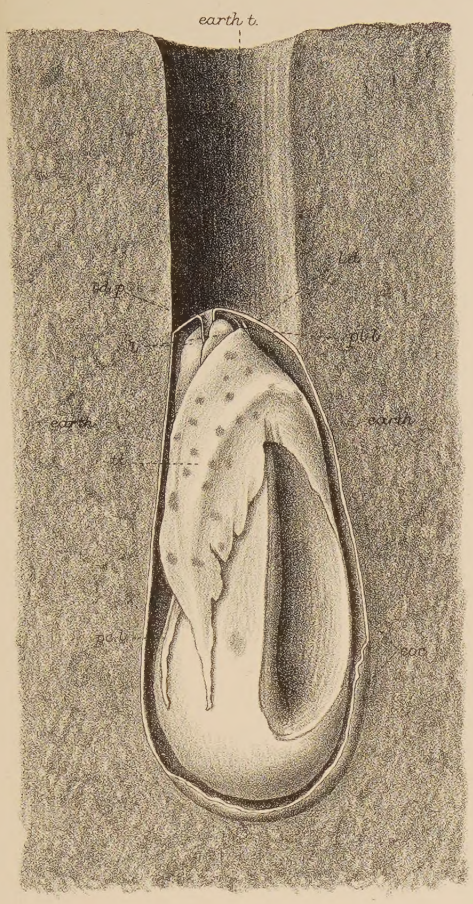
67. Diagram of the torpid *Protopterus annectens, in situ.* The earth and wall of the capsule are removed on one side.

68. Figure of entire capsule, or cocoon.

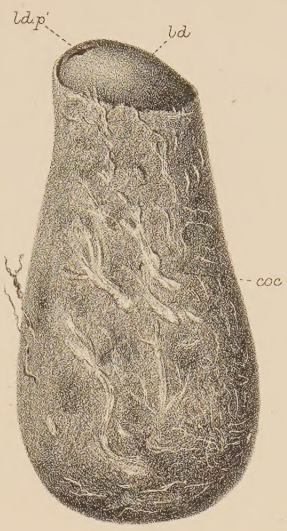
69. "Lid" of capsule, from the outer side.

70. Head of *Protopterus annectens.*

71. Diagram of the brachial plexus (the first spinal nerve only is shown).



67.



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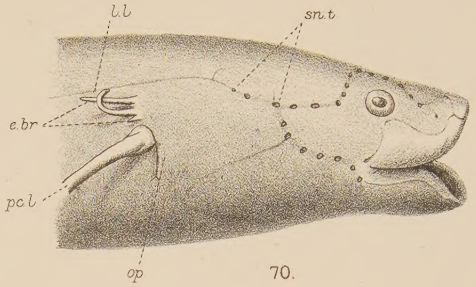
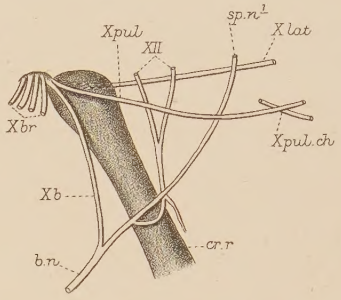


70.



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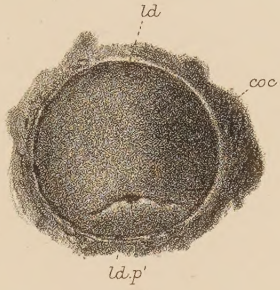

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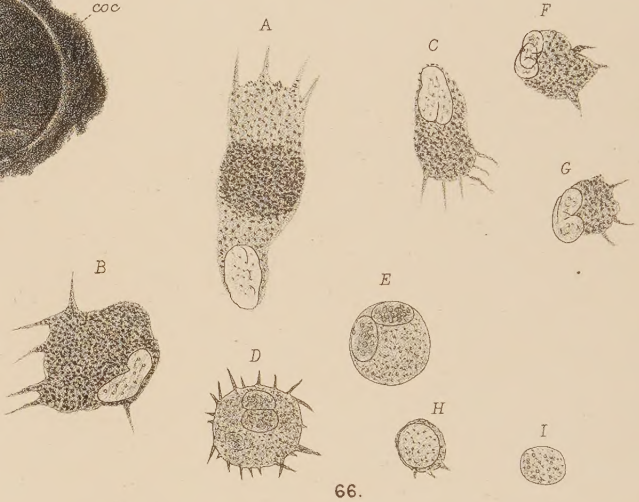
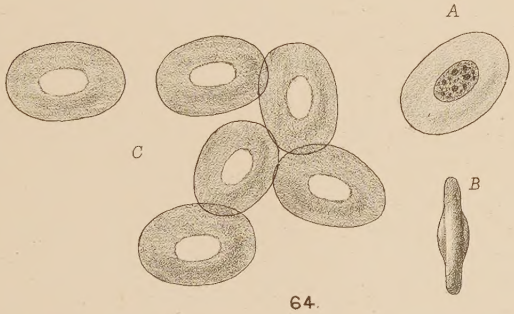
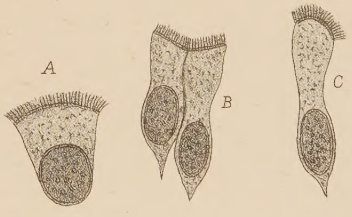


66.



64.



65.

63.

W.N.P., T.H.T. & L.B.C. del. ad nat.
M.P. Parker chromo-lith.
West, Newman imp.